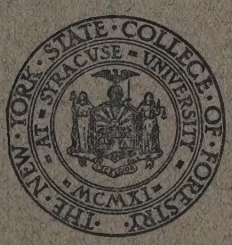
Volume XVIII June, 1918 Number 5

TECHNICAL PUBLICATION NO. 11
OF
THE NEW YORK STATE COLLEGE OF FORESTRY
AT
SYRACUSE UNIVERSITY
HUGH P. BAKER, Dean

The Biology of Polyporus Pargamenus Fries

BY
ARTHUR S. RHOADS



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THE BIOLOGY OF POLYPORUS PARGAMENUS Fries.

A THESIS

Submitted to the Faculty of the New York State College of Forestry at Syracuse University in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy, May 1, 1917.

BY

Arthur S. Rhoads, M. S.

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THE BIOLOGY OF POLYPORUS PARGAMENUS Fries.[1]

ARTHUR S. RHOADS.

Introduction.

Polyporus[2] *pargamenus* Fries is one of the numerous fungi which cause the rotting of wood. Its small sporophores are to be found during all months of the year on living trees, dead trees, and fallen woody parts in moist situations. Even in winter its sporophores begin to grow with every warm spell of weather. Under the climatic conditions of the eastern United States, however, it is especially during the autumn months that the sporophores appear in great abundance. This fungus is one of the familiar objects to the field mycologist, but its life history, morphology, and ecology seem hitherto to have been neglected.

Deciduous forest trees are effected with an unusually large number of different fungous diseases, some of which are assuming more and more importance daily. In dealing with our timber tracts, whether they be wood-lots or larger areas, it is becoming of increasing importance to take cognizance of those factors which entail a marked depreciation in the

[1] A thesis submitted to the faculty of The New York State College of Forestry at Syracuse University in partial fulfillment of the requirements for the degree of Doctor of Philosophy, May 1, 1917.

[2] The writer has deemed it advisable to drop the generic name *Polystictus* as a designation of a section of *Polyporus* for two reasons: First, because it is a synonym of *Coltricia* Gray, which was proposed several years earlier, and second, because it is not a well-defined genus, there being too many intermediate species to permit of its being longer used. This digression should cause no confusion since the names *Polyporus* and *Polystictus* have been used almost interchangeably with reference to the thin coriaceous plants once segregrated under the latter name.

value of the timber produced, either by diminishing the value of the wood cut or by retarding or preventing the growth of the trees themselves.

Polyporus pargamenus, while of rare occurrence on coniferous woods, grows on all or nearly all of the dicotyledonous woods occurring within its range, especially on the sapwood, and exhibits no perceptible preference for any particular species. On account of its wide geographic distribution and its ability to grow on and destroy so many different kinds of wood it should be regarded, in the United States at least, as second probably only to its near relative, *Polyporus versicolor* (L.) Fr., in being the most common of the wood-destroying fungi which attack the dead wood of dicotyledonous trees. As a usual rule *Polyporus pargamenus* is confined to dead trees and fallen woody parts, although frequently it may become a wound parasite and thus attack living trees whenever they become injured. The decay is at first restricted to the sapwood, but, under favorable conditions, after the destruction of the sapwood the fungus may advance and gradually decay the heartwood also. Thus the whole tree may be rendered valueless for lumber and of but little value for fuel. To the living forest trees, therefore, this class of fungi is a constant menace, and to the dead trees and fallen trunks, almost a certain evil.

These saprophytes are of great importance in two ways. From the standpoint of man's narrower economy they are directly injurious by virtue of the enormous losses sustained as a result of the decay of wood and timbers. From the standpoint of the broader economy of nature they are the scavengers which retard the accumulation of plant débris. As such their ability vastly outweighs those effects detrimental to man's interest.

It was not until 1833 that we had the first attempt, by Theodor Hartig, at a scientific investigation of the decay of wood. Of course the earlier explanations of the causes of disease were bound to be defective in accordance with the condition of botanical science at that time, but with the advent of time the basic principles became established

effectually. As a result of the increasing favor with which this phase of plant pathology has met, an extensive literature on the subject has been assembled gradually. Despite our rapid progress in certain fields, we as yet know but little concerning the life histories of our wood-destroying fungi, supplemented by detailed and accurate information as to the way in which they bring about decay in wood, together with the chemistry involved in the process of decay. The prevention of the destruction of wood by any particular fungus presupposes a definite knowledge of its biologic and physiologic relations. Since we still are lacking this knowledge for the species here selected for investigation, detailed studies have been undertaken, placing foremost the interests of dendropathology and technical science.

Geographic Distribution and Host Woods of Polyporus Pargamenus.

Polyporus pargamenus is of wide geographic distribution, occurring on most any of the dicotyledonous, although rarely the coniferous, trees in many parts of the world. In the United States this fungus is of especially common occurrence in the great deciduous forests east of the Mississippi River, but of only scattered occurrence throughout the states west of the Mississippi River. Even here its occurrence in most all the states would lead one to expect that it will be reported eventually from every state, since *Populus tremuloides* Michx., which occurs in all of the western states, serves as a host to bridge the prairie states, *Polyporus pargamenus* having been collected on this species from points as far west as North Dakota, Colorado, and New Mexico. Collections of this fungus have been recorded from all states of the United States but Nebraska, Wyoming, Nevada, California, and Arizona. From the United States *Polyporus pargamenus* extends northward into southern Canada, authentic collections being recorded from British Columbia, Ontario, Quebec, Nova Scotia, and Newfoundland. The fungus likewise extends southward through Mexico and Central America.

Murrill (1915, p. 17) states that *Polyporus pargamenus* is frequent to common on dead wood throughout most of tropical North America, including Mexico, Central America, southern Florida, the Bermudas, the West Indies, and all other islands between North America and South America with the exception of Trinidad. Hans and Paul Sydow (1907) record it from South America as being among the collections of F. Noak made in Brazil. According to Murrill (1906, p. 655), Bresadola reports it as being common on poplar, oak, and basswood in Hungary and considers it cosmopolitan in one or more of its multiplied forms.

Authentic collections of *Polyporus pargamenus* have been recorded from Spain, France, Germany, Austria-Hungary, and Russia in Europe; from Japan, Malay Peninsula, and the Philippine Islands in Asia; and from Queensland and Victoria in Australia.

From the foregoing facts it is evident that the distribution of *Polyporus pargamenus,* even though still known but very imperfectly, embraces five of the six continents. A detailed tabulation of all the more important authentic collections of *Polyporus pargamenus* that the writer has been able to compile is given in the following pages. In connection with this work the specimens in the herbaria of the New York Botanical Garden, The Pennsylvania State College, the Office of Pathological Collections of the U. S. Bureau of Plant Industry, and the collections of the Office of Investigations in Forest Pathology having been examined personally.

Distribution in North America.

CANADA.

British Columbia:

On ——————. Kamloops, J. Macoun, in June, 1889 (Herb. N. Y. Bot. Gard.); New Westminster (Herb. N. Y. Bot. Gard.); Sidney, J. Macoun (Herb. C. G. Lloyd, No. 13089).

Ontario:

On *Populus* sp. London, J. Dearness, in August, 1887 (Herb. N. Y. Bot. Gard.).

On *Quercus rubra.* Ontario (Herb. N. Y. Bot. Gard.).

ONTARIO — *Continued:*

On *Acer* sp. Crystal Beach, E. Bartholomew, in July, 1913 (Fungi Columbiani, No. 4913).

On ————————. Shannonville, in 1882 (Herb. N. Y. Bot. Gard.); London, J. Dearness (Herb. C. G. Lloyd, No. 11172); Simcoe, P. L. Ricker (Herb. C. G. Lloyd, No. 05065½; Temagami, C. G. Lloyd (Herb. C. G. Lloyd, No. 07616); Toronto, Thos. Langton (Herb. C. G. Lloyd, Nos. 08 + 302, and 05260); Locality unknown, Mrs. I. M. Walker (Herb. C. G. Lloyd, No. 05577).

QUEBEC:

On ————————. Little Metis, J. Fowler (Herb. C. G. Lloyd, No. 08 + 133); Montreal, H. Dupret (Herb. C. G. Lloyd, No. 05479).

NOVA SCOTIA:

On *Populus balsamifera.* Pictou, Robinson, in August, 1905 (Herb. N. Y. Bot. Gard.).

On ————————. Halifax, A. H. Mackay, in November, 1906 (Herb. N. Y. Bot. Gard.).

NEWFOUNDLAND:

On *Betula* sp. Locality unknown, A. C. Waghorne, in August, 1897 (Herb. N. Y. Bot. Gard.).

On ————————. Locality unknown, A. C. Waghorne, in 1887 (Herb. Mo. Bot. Gard., No. 4558).

UNITED STATES.

ALABAMA:

On *Quercus nigra.* Auburn, in January, 1897 (Herb. Mo. Bot. Gard., No. 4437).

On *Liquidambar styraciflua.* Dothan, G. G. Hedgcock, in March, 1915 (F. P.[3] 17580).

On *Ilex opaca.* Auburn, Peters (Herb. N. Y. Bot. Gard.).

On *Rhododendron maximum.* Goldbranch, J. R. Weir, in 1904 (Herb. J. R. Weir, No. 9593).

On ————————. Auburn, F. S. Earle, in December, 1896 (Herb. N. Y. Bot. Gard.); Auburn, in February, 1897 (Herb. Mo. Bot. Gard., No. 4436); Montgomery, J. D. Burke (Herb. C. G. Lloyd, No. 7).

ARKANSAS:

On *Quercus alba.* Rogers, E. Bartholomew, in October, 1908 (Fungi Columbiani, No. 2825).

On *Quercus marilandica.* Nordyce, C. J. Humphrey, in September, 1909 (F. P. 5601).

[3] "F. P." = Forest Pathology Investigations number.

ARKANSAS — *Continued:*

On *Liquidambar styraciflua.* Camden, C. J. Humphrey, in September, 1909 (F. P. 6180); El Dorado, T. C. Abbott, in December, 1914 (F. P. 2879).

On ————————. Wynne, Wm. Trelease, in March, 1899 (Herb. Mo. Bot. Gard., No. 4431).

COLORADO:

On *Populus tremuloidcs.* Montezuma National Forest, G. G. Hedgcock, in July, 1911 (F. P. 9268); San Juan National Forest, G. G. Hedgcock, in July, 1911 (F. P. 9224).

On *Alnus tenuifolia.* Golden, L. O. Overholts, in 1914 (Herb. L. O. Overholts, No. 1743).

On ————————. Denver, E. Knaebel (Herb. C. G. Lloyd, No. 07663).

CONNECTICUT:

On *Betula alba.* Central Village, J. L. Sheldon, in September, 1910 (F. P. 9104).

On *Betula lutea.* North Bloomfield, P. Spaulding, in September, 1910 (F. P. 2295).

On *Quercus* sp. J. L. Sheldon, in August, 1908 (F. P. 9105).

On *Acer saccharinum.* Junction of Moosup and Quinnebaug Rivers, J. L. Sheldon, in September, 1908 (F. P. 9103).

DELAWARE:

On *Acer rubrum.* Wilmington (Herb. N. Y. Bot. Gard.).

DISTRICT OF COLUMBIA:

On *Castanea dentata.* Washington, S. C. Bruner, in February, 1914 (F. P. 8269).

On *Quercus prinus.* Takoma Park, R. G. Pierce, in November, 1913 (F. P. 18003).

On *Tilia platyphyllos.* Washington, G. G. Hedgcock (?), (F. P. 462 a).

On ————————. Washington, H. R. Ramsey, in October, 1915 (Herb. Path. Coll.).

FLORIDA:

On *Hicoria* sp. Jacksonville, G. G. Hedgcock, in March, 1918 (F. P. 23674).

On *Liquidambar styraciflua.* Gainesville, G. G. Hedgcock, in March, 1915 (F. P. 17303); Jacksonville, G. G. Hedgcock, in March 1918.

On ————————. Eustis, G. V. Nash, in July, 1895 (Herb. Mo. Bot. Gard., No. 4557); Gainesville, N. L. T. Nelson (Herb. C. G. Lloyd, Nos. 13, 37, 176, and 191); H. S. Fawcett (Herb. C. G. Lloyd, No. 08089).

GEORGIA:

On *Fagus atropunicea*. Atlanta, E. Bartholomew, in November, 1914 (Fungi Columbiani, No. 4522).

On *Liquidambar styraciflua*. Darien, H. W. Ravenel, in March, 1881 (Ellis' N. A. Flora, No. 312 d); Savannah, C. J. Humphrey, in July, 1909 (F. P. 5074).

On *Nyssa aquatica*. Near Macon, R. M. Harper, in 1902 (Georgia Plants, No. 1805 b).

On ————————. Bullock Co., R. M. Harper, in June, 1901 (Ellis' N. A. Flora, No. 884 d); Locality unknown, H. H. Bartlet (Herb. C. G. Lloyd, Nos. 08 + 210, and 08 + 211); Cornelia, G. C. Fitch (Herb. C. G. Lloyd, No. 12814); Vienna, C. J. Humphrey, in July, 1909 (F. P. 5153).

IDAHO:

On *Populus tremuloides*. Salmon National Forest, G. G. Hedgcock, in August, 1910 (F. P. 4483); Priest River, J. R. Weir, in September, 1915 (Herb. J. R. Weir, No. 700).

On *Populus acuminata*. Salmon National Forest, G. G. Hedgcock, in August, 1910 (F. P. 4480).

On *Populus trichocarpa*. Priest River, J. R. Weir, in September, 1914 (Herb. J. R. Weir, No. 702).

On *Betula occidentalis*. Priest River, J. R. Weir, in September, 1914 (Herb. J. R. Weir, No. 697).

ILLINOIS:

On *Quercus alba*. Jacksonville, E. Bartholomew, in September, 1907 (Fungi Columbiani, No. 2513).

On *Quercus prinus*. Cobden (Herb. N. Y. Bot. Gard.).

On *Quercus* sp. Cobden, F. S. Earle, in March, 1887 (Herb. Path. Coll.); Edgemont, L. O. Overholts, in 1912 (Herb. L. O. Overholts, No. 594); Cerro Gordo, L. O. Overholts, in 1915 (Herb. L. O. Overholts, No. 3213).

On ————————. Grand Pass, Trelease, in March, 1899 (Herb. Mo. Bot. Gard., No. 4433); Joliet (Herb. C. G. Lloyd, No. 05298); Chicago, L. H. Watson (Herb. C. G. Lloyd, No. 05333).

INDIANA:

On *Salix nigra*. Scottsburg, J. R. Weir, in May, 1912 (Herb. J. R. Weir, No. 693).

On *Hicoria glabra*. Scottsburg, J. R. Weir, in May, 1912 (Herb. J. R. Weir, No. 703).

On *Fagus atropunicea*. Weirtown, J. R. Weir, in 1912 (Herb. L. O. Overholts, No. 3529).

On *Quercus rubra*. Weirtown, J. R. Weir, in May, 1912 (Herb. J. R. Weir, No. 696).

On *Toxylon pomiferum*. Little York, J. R. Weir, in November, 1917 (Herb. J. R. Weir, No. 5211).

INDIANA — *Continued:*

On *Prunus serotina*. Brownstown, J. R. Weir, in April, 1912 (Herb. J. R. Weir, No. 692).

On *Cercis canadensis*. Weirtown, J. R. Weir, in November, 1906 (Herb. J. R. Weir, No. 5215).

On *Gleditsia triacanthos*. Scottsburg, J. R. Weir, in November, 1917 (Herb. J. R. Weir, No. 9556).

IOWA:

On ————————. Decorah, E. M. Holway (?), in June, 1882 (Herb. N. Y. Bot. Gard.); Ft. Dodge, O. M. Oleson (Herb. C. G. Lloyd, Nos. 383, 561 a, 12174, and 12720).

KANSAS:

On *Quercus* sp. Bourbon Co., A. O. Garret, in August, 1902 (Herb. E. A. Burt).

On *Ulmus americana*. Strong City, G. G. Hedgcock, in November, 1910 (F. P. 4947).

On ————————. Manhattan, Kellerman and Swingle, in August, 1897 (Kansas Fungi, No. 1091); Rockport, E. Bartholomew (Herb. C. G. Lloyd, No. 6038).

KENTUCKY:

On *Quercus alba*. Ft. Thomas, J. R. Weir, in April, 1912 (Herb. J. R. Weir, No. 699).

On *Quercus* sp. Berea, L. O. Overholts, in 1915 (Herb. L. O. Overholts, No. 2767).

On *Tilia americana*. Louisville, J. R. Weir, in April, 1912 (Herb. J. R. Weir, No. 685).

On ————————. Mammoth Cave, C. G. Lloyd, in June, 1896 (Herb. Mo. Bot. Gard., No. 4439); Crittenden, C. G. Lloyd (Herb. C. G. Lloyd, Nos. 001, 0014, 07079, 1222, and 07355).

LOUISIANA:

On *Pinus* sp. East Louisiana, March, 1886 (Herb. Path. Coll.).

On *Salix* sp. Baton Rouge, C. J. Humphrey, in August, 1909 (F. P. 5428).

On *Quercus virginiana*. New Orleans, G. G. Hedgcock, in March, 1909 (F. P. 343).

On *Quercus palustris*. Bogalusa, G. G. Hedgcock, in March, 1909 (F. P. 367, 392, and 409).

On *Quercus nigra*. Baton Rouge, C. J. Humphrey, in August, 1909 (F. P. 5393).

On *Ulmus* sp. Locality and collector unknown, in November, 1889 (Herb. Path. Coll.).

On *Nyssa sylvatica*. Locality unknown, G. G. Hedgcock, in March, 1909 (F. P. 709).

LOUISIANA — *Continued:*

On ————————. Ville Platte, A. B. Langlois, in May, 1886 (Herb. Path. Coll.); Slidell, C. J. Humphrey, in July, 1909 (F. P. 5376).

MAINE:

On *Salix* sp. Kittery Point, A. S. Rhoads, in April, 1918.

On *Populus tremuloides.* Kittery Point, A. S. Rhoads, in June, 1918.

On *Betula populifolia.* Kittery Point, A. S. Rhoads, in April, 1918; in July, 1918 (F. P. 23681).

On *Betula lutea.* Hastings, G. G. Hedgcock, in July, 1913 (F. P.).

On ————————. Orono (Fungi of N. A., No. 140 a).

MARYLAND:

On *Pinus virginiana.* Takoma Park, A. S. Rhoads, in November, 1917 (F. P. 23651).

On *Betula nigra.* Takoma Park, G. G. Hedgcock, in September, 1908 (F. P. 4020); Great Falls, A. S. Rhoads, in October, 1917 (F. P. 23650); Cabin John Creek, A. S. Rhoads, in November, 1917 (F. P. 23656).

On *Carpinus caroliniana.* Takoma Park, A. S. Rhoads, in November, 1917 (F. P. 23649); Cabin John Creek, A. S. Rhoads, in November, 1917.

On *Fagus atropunicea.* Cabin John Creek, A. S. Rhoads, in November, 1917.

On *Castanea dentata.* Takoma Park, G. G. Hedgcock, in September, 1908 (F. P. 253 and 411); in 1909 (F. P. 467).

On *Quercus alba.* Takoma Park, G. G. Hedgcock, in April, 1911 (F. P. 9006).

On *Quercus prinus.* Cabin John Creek, A. S. Rhoads, in November, 1917.

On *Quercus rubra.* Glen Echo, A. S. Rhoads, in August, 1917; Great Falls, A. S. Rhoads, in October, 1917.

On *Quercus palustris.* Cabin John Creek, A. S. Rhoads, in October, 1917.

On *Liriodendron tulipifera.* Takoma Park, G. G. Hedgcock, in June, 1910 (F. P. 4001 and 4006); Glen Echo, A. S. Rhoads, in August, 1917.

On *Prunus serotina.* Chain Bridge, A. S. Rhoads, in October, 1917.

On *Acer rubrum.* Great Falls, A. S. Rhoads, in October, 1917; Cabin John Creek, A. S. Rhoads, in November, 1917.

MASSACHUSETTS:

On *Salix* sp. Mt. Auburn, E. A. Burt, in November, 1893 (Herb. E. A. Burt).

MASSACHUSETTS — *Continued:*

On *Hicoria* sp. Mt. Holyoke, P. Spaulding, in September, 1912 (F. P. 2746).

On *Betula lutea.* Mt. Holyoke, P. Spaulding, in September, 1912 (F. P. 2743).

MICHIGAN:

On *Populus* sp. Houghton, L. H. Pennington, in July, 1906 (Herb. L. H. Pennington).

On *Betula papyrifera.* Marquette, L. H. Pennington, in August, 1906 (Herb. L. H. Pennington).

On *Betula lenta.* Locality and collector unknown (Herb. N. Y. Bot. Gard.).

On *Platanus occidentalis.* Reported by C. H. Kauffman (1917, p. 156).

On ————————. Ann Arbor, C. H. Kauffman (Herb. C. G. Lloyd, Nos. 45 and 10590); Detroit, O. E. Fischer (Herb. C. G. Lloyd, No. 10328).

MINNESOTA:

On *Populus tremuloides.* Cass Lake, G. G. Hedgcock, in July, 1910 (F. P. 4171); Park Rapids, G. G. Hedgcock, in July, 1910 (F. P. 4161); Itasca Lake, G. G. Hedgcock, in July, 1910 (F. P. 4095); Minnetonka Lake, G. G. Hedgcock, in July, 1910 (F. P. 4064 and 4066).

On *Populus grandidentata.* Cass Lake, R. G. Pierce, in June, 1915 (F. P. 18068).

On *Populus balsamifera.* Cass Lake, J. R. Weir, in June, 1912 (Herb. J. R. Weir, No. 701).

On *Betula papyrifera.* Lake Itasca, G. G. Hedgcock, in July, 1910 (F. P. 4091 and 4125); Cass Lake, G. G. Hedgcock, in July, 1910 (F. P. 4201); J. R. Weir, in June, 1912 (F. P.).

On *Quercus coccinea.* Lake Minnetonka, G. G. Hedgcock, in July, 1910 (F. P. 4070).

On *Tilia americana.* Cass Lake, J. R. Weir, in June, 1912 (Herb. J. R. Weir, No. 694).

MISSISSIPPI:

On *Persea pubescens.* Sandy Hook, G. G. Hedgcock, in March, 1909 (F. P.).

On ————————. Biloxi, O. M. Oleson (Herb. C. G. Lloyd, No. 579).

MISSOURI:

On *Hicoria* sp. Creve Coeur, P. Spaulding, in December, 1905 (Herb. Mo. Bot. Gard.).

On *Betula nigra.* Williamsville, B. M. Duggar, in October, 1902 (Herb. E. A. Burt).

MISSOURI — *Continued:*

On *Quercus velutina.* Perryville, C. H. Demetrio, in April, 1883 (Rabenhorst-Winter's Fungi Europaei, No. 3331).

On *Quercus* sp. Jefferson Barracks, L. O. Overholts, in 1913 (Herb. L. O. Overholts, No. 529); Bismark, L. O. Overholts, in December, 1913 (Herb. Mo. Bot. Gard., Nos. 1780 and 21994).

On *Prunus* sp. Perryville, L. O. Overholts, in 1915 (Herb. L. O. Overholts, No. 2704).

On ————————. O'Fallon, Wm. Trelease, in November, 1895 (Herb. Mo. Bot. Gard., No. 4714); Valley Park, H. von Schrenk, in October, 1896 (Herb. Mo. Bot. Gard., No. 42838); Cliff Cave, J. B. S. Norton, in April, 1898 (Herb. Mo. Bot. Gard. No. 3864); Meramec, P. Spaulding, in April, 1906 (Herb. Mo. Bot. Gard., No. 4186); Poplar Bluff, F. W. Dewart(?), in August, 1892 (Herb. Mo. Bot. Gard., No. 4086); Creve Coeur Lake, L. O. Overholts, in 1912 (Herb. L. O. Overholts, No. 482).

MONTANA:

On *Salix lasiandra.* Belton, J. R. Weir, in September, 1912 (Herb. J. R. Weir, No. 691).

On *Populus trichocarpa.* Ashland, J. R. Weir, in September, 1913 (Herb. J. R. Weir, No. 690); Wisdom, J. R. Weir, in September, 1914 (Herb. J. R. Weir, No. 688).

On *Alnus tenuifolia.* Missoula, J. R. Weir, in May, 1914 (Herb. J. R. Weir, No. 689).

NEW HAMPSHIRE:

On *Juglans cinerea.* North Conway, A. S. Rhoads, in August, 1918 (Herb. A. S. Rhoads).

On *Salix discolor.* North Conway, A. S. Rhoads, in August, 1918 (Herb. A. S. Rhoads and F. P. 23684).

On *Populus tremuloides.* Willey House, A. S. Rhoads, in August, 1918 (Herb. A. S. Rhoads); North Conway, A. S. Rhoads, in September, 1918 (Herb. A. S. Rhoads).

On *Betula lutea.* Gorham, G. G. Hedgcock, in July, 1913 (F. P. 8608).

On *Betula papyrifera.* Gorham, P. Spaulding, in September, 1910 (F. P. 2319); North Conway, A. S. Rhoads, in September, 1918.

On *Fagus atropunicea.* Willey House, A. S. Rhoads, in August, 1918; North Conway, A. S. Rhoads, in August, 1918.

On *Prunus pennsylvanica.* Gorham, G. G. Hedgcock, in July, 1913 (F. P. 8645).

On *Acer saccharum.* White Mountains, G. G. Hedgcock, in July, 1913 (F. P. 8628).

On *Acer pennsylvanicum.* Gorham, P. Spaulding, in September, 1910 (F. P. 2342).

On *Acer rubrum.* North Conway, A. S. Rhoads, in September, 1918 (Herb. A. S. Rhoads).

NEW JERSEY:

On ————————. Newfield, J. B. Ellis, in November, 1876 (Mycotheca Universalis, No. 1304); Ellis and Everhart (Fungi Columbiani, No. 302); Trenton, E. B. Sterling (Herb. C. G. Lloyd, Nos. 08 + 452, 08 + 492, 08 + 459, 08 + 499, 05844, and 07656).

NEW MEXICO:

On *Populus tremuloides*. Manzano National Forest, G. G. Hedgcock, in June, 1908 (F. P.); Mogollen, G. G. Hedgcock and W. H. Long, in October, 1911 (F. P. 9888); Sandia Mts., G. G. Hedgcock, in June, 1908 (F. P. 456 and 462).

NEW YORK:

On *Tsuga canandensis*.. Ithaca, B. B. Higgins, in October, 1911 (Fungi Columbiani, No. 3616); Jamesville, A. S. Rhoads, in November, 1915 (Herb. A. S. Rhoads).

On *Hicoria glabra*. Syracuse, A. S. Rhoads, in November, 1916.

On *Hicoria minima*. Jamesville, A. S. Rhoads, in October, 1916.

On *Populus tremuloides*. Center, C. H. Peck, in September, 1879 (Ellis' N. A. Fungi, No. 312 a); Saranac, P. Spaulding, in May, 1909 (F. P. 2041); Glenn Falls, G. G. Hedgcock, in August, 1913 (F. P. 8660); Dobson's Camp, A. S. Rhoads, in June, 1916 (Herb. A. S. Rhoads).

On *Populus grandidentata*. Jamesville, A. S. Rhoads, in October, 1916.

On *Betula lutea*. Copake, C. H. Peck, in October, 1877 (Mycotheca Universalis, No. 1102); Cranberry Lake, A. S. Rhoads, in July, 1916; Fayetteville and Jamesville, A. S. Rhoads, in October, 1916.

On *Betula papyrifera*. Glenn Falls, G. G. Hedgcock, in August, 1913 (F. P. 8666).

On *Fagus atropunicea*. Alcove, C. L. Shear, in August, 1893 (Shear's New York Fungi, No. 38); Apulia, A. S. Rhoads, in September, 1916.

On *Castanea dentata*. Verona, C. H. Peck, in August, 1879 (Ellis' N. A. Fungi, No. 312 b).

On *Quercus alba*. Glenn Falls, G. G. Hedgcock, in August, 1913 (F. P. 8663).

On *Quercus rubra*. Glenn Falls, G. G. Hedgcock, in August, 1913 (F. P. 8662).

On *Prunus serotina*. Apulia, A. S. Rhoads, in October, 1916.

On *Prunus pennsylvanica*. Phoenix, A. S. Rhoads, in September, 1916.

On *Acer saccharum*. Cranberry Lake and Jamesville, A. S. Rhoads, in August, 1916.

On *Acer pennsylvanicum*. Cranberry Lake, A. S. Rhoads, in July, 1916.

On ————————. Long Island, G. C. Fisher (Herb. C. G. Lloyd, No. 08 + 238).

NORTH CAROLINA:

On *Hicoria glabra.* Bald Rock, A. H. Graves, in August, 1910 (F. P. 3687); Fairfield Lake, in August, 1910 (F. P.).

NORTH CAROLINA — *Continued:*

On *Fagus atropunicea.* Salem, R. K. Beattie, in February, 1913 (F. P. 8233).

On *Acer rubrum.* Marion, A. Ames, in October, 19— (F. P.).

On *Quercus* sp. Leicester, B. B. Higgins, in July, 1909 (Fungi Columbiani, No. 2924).

NORTH DAKOTA:

On *Populus tremuloides.* Near Fargo, J. F. Brenckle and O. A. Stevens, in June 1915 (Fungi Dakotensis, No. 412).

OHIO:

On *Betula* sp. East Cleveland, E. Claassen, in 1911 (Herb. L. O. Overholts, No. 269).

On *Quercus* sp. West Elkton, L. O. Overholts, in 1912 (Herb. L. O. Overholts, No. 476).

On *Prunus* sp. Lorain Co., E. C. Mosely, in 1911 (Herb. L. O. Overholts, No. 318).

On *Acer* sp. Oxford, L. O. Overholts, in 1909 (Herb. L. O. Overholts, No. 6).

On ————————. Cincinnati, D. L. James, in October, 1879 (Ellis' N. A. Fungi, No. 312 c); Oxford, L. O. Overholts, in 1910 (Herb. L. O. Overholts, No. 7); Sugar Grove, W. G. Stover, in 1911 (Herb. L. O. Overholts, No. 166).

OKLAHOMA:

On ————————. Poteau, I. T., Wm. Trelease, in February, 1901 (Herb. Mo. Bot. Gard., No. 4732).

OREGON:

On *Quercus californica.* Grants Pass, J. R. Weir, in September, 1916 (Herb. J. R. Weir, No. 686).

On *Quercus garryana.* Portland, J. R. Weir, in August, 1913 (Herb. J. R. Weir, No. 698).

PENNSYLVANIA:

On *Tsuga canandensis.* Philadelphia, A. S. Rhoads, in September, 1916 (Herb. Penna. State College).

On *Hicoria alba.* Near State College, A. S. Rhoads, in 1913 (Herb. Penna. State College); A. S. Rhoads, in September, 1916.

On *Hicoria ovata.* Lemont, C. R. Orton and A. S. Rhoads, in 1915 (Herb. Penna. State College).

On *Betula lenta.* Near State College, A. R. Bechtel, in 1913 (Herb. Penna. State College); Philadelphia, A. S. Rhoads, in September, 1916.

On *Betula lutea.* Carbondale, E. A. Burt, in December, 1898 (Herb. E. A. Burt); near State College, A. S. Rhoads, in 1915 (Herb. Penna. State College).

PENNSYLVANIA — *Continued:*

On *Castanea dentata.* Near State College and Ephrata, A. S. Rhoads, in September, 1916.

On *Quercus alba.* Near State College, A. S. Rhoads, in 1914 (Herb. Penna. State College); A. S. Rhoads, in September, 1916.

On *Quercus phellos.* Philadelphia, A. S. Rhoads, in September, 1916.

On *Quercus prinus.* Ephrata and Philadelphia, A. S. Rhoads, in September, 1916 (Herb. A. S. Rhoads).

On *Quercus coccinea.* Near State College, A. S. Rhoads, in September, 1916.

On *Quercus velutina.* Philadelphia, A. S. Rhoads, in 1915 (Herb. Penna. State College).

On *Prunus* sp. Petersburg, G. G. Hedgcock, in June, 1914 (F. P. 15478).

On *Gleditsia triacanthos.* State College, C. R. Orton and L. O. Overholts, in 1916 (Herb. Penna. State College).

On *Acer rubrum.* Mont Alto, J. S. Illick, in May, 1913 (F. P. 8346); Hammersley Forks, M. E. Muller, in January, 1914 (F. P. 15248); near Boalsburg, A. S. Rhoads, in 1915 (Herb. Penna. State College); State College and Philadelphia, A. S. Rhoads, in September, 1916.

RHODE ISLAND:

Locality and other data unknown. Several collections in herbarium of Brown University.

SOUTH CAROLINA:

On *Hicoria* sp. Aiken, H. W. Ravenel (Fungi Americani Exicatti, No. 423).

On *Nyssa* sp. Lanes, C. J. Humphrey, in July, 1909 (F. P. 5040).

On ————————. Locality unknown, H. W. Ravenel, in 1852 (Fungi Caroliniani, Fasc. I, No. 13).

SOUTH DAKOTA:

On *Populus tremuloides.* Custer, G. G. Hedgcock, in September, 1914 (F. P. 15818).

TENNESSEE:

On *Quercus* sp. Jonesboro (Herb. N. Y. Bot. Gard.).

On ————————. Rugby, M. S. Percival (Herb. C. G. Lloyd. Nos. 7142 and 10831).

TEXAS:

On *Quercus nigra.* Quitman, W. H. Long, in November, 1911 (F. P. 12089).

On *Quercus texana.* Houston, G. G. Hedgcock, in March, 1909 (F. P. 722).

On *Liquidambar styraciflua.* Joaquin, E. Bartholomew, in October, 1913 (Fungi Columbiani, No. 4620); Quitman, W. H. Long, in November, 1911 (F. P. 12051).

TEXAS — *Continued:*

On *Nyssa sylvatica.* Houston, G. G. Hedgcock, in March, 1909 (F. P. 701).

UTAH:

On ————————. Locality unknown (as *Coriolus subchartaceus* Murrill *in* North Am. Fl. **9**:24, 1907.

VERMONT:

On *Populus tremuloides.* Bethel, P. Spaulding, in May, 1908 (F. P. 2067).

On *Populus grandidentata.* Bethel, P. Spaulding, in May, 1909 (F. P. 2186).

On *Betula lutea.* Middlebury, E. A. Burt, in October, 1895 (Herb. E. A. Burt); Bethel, P. Spaulding, in November, 1912 (F. P. 2561); Walden, C. R., Orton, in 1913 (Herb. Penna. State College).

On *Prunus* sp. Bethel, P. Spaulding, in January, 1912 (F. P. 2573).

On *Acer saccharum.* Bethel, P. Spaulding, in October, 1910 (F. P. 2423).

On *Acer saccharinum.* Bethel, P. Spaulding, in November, 1912 (F. P. 2711).

VIRGINIA:

On *Betula nigra.* Great Falls, P. Spaulding, in January, 1911 (F. P. 2395).

On *Quercus prinus.* Rosslyn, R. G. Pierce, in December, 1914 (F. P.).

On *Quercus velutina.* Rio, G. F. Gravatt, in February, 1915 (F. P. 17281).

On *Quercus rubra.* Chain Bridge, A. S. Rhoads, in October, 1917.

On *Quercus marilandica.* Chain Bridge, A. S. Rhoads, in October, 1917.

On *Sassafras sassafras.* Chain Bridge, A. S. Rhoads, in October, 1917 (F. P. 23643).

On *Prunus americana.* Chain Bridge, A. S. Rhoads, in October, 1917 (F. P. 23642).

On *Prunus serotina.* Chain Bridge, A. S. Rhoads, in October, 1917.

On *Rhus vernix.* Vienna, A. S. Rhoads, in January, 1918 (Herb. A. S. Rhoads).

On *Acer rubrum.* Chain Bridge, A. S. Rhoads, in October, 1917.

On *Fraxinus americana.* Great Falls, P. Spaulding, in January, 1911 (F. P. 2461).

WASHINGTON:

On *Quercus garryana.* Near Bellingham, J. R. Weir, in September, 1916 (Herb. J. R. Weir, No. 687).

WEST VIRGINIA:

On *Betula* sp. Cranberry Glades, Pocahontas Co., J. L. Sheldon, in August, 1909 (Fungi Columbiani, No. 3655).

WEST VIRGINIA — *Continued:*

On *Fagus atropunicea*. Albright, J. L. Sheldon, in August, 1908 (F. P. 9102).

On *Quercus* sp. Cranberry Glades, Pocahontas Co., J. L. Sheldon, in August, 1909 (Fungi Columbiani, No. 3621).

WISCONSIN:

On *Salix* sp. Madison, M. C. Jensen, in October, 1910 (F. P. 6711).

On *Populus* sp. Oneida Co., J. J. Neuman, in 1904 (Herb. Mo. Bot. Gard., No. 42712).

On *Betula papyrifera*. Trout Lake, P. Spaulding, in June, 1915 (F. P. 2691).

On *Quercus* sp. Madison, C. J. Humphrey and E. Bartholomew, in October, 1911 (Fungi Columbiani, No. 3907).

On *Alnus incana*. Elmside, R. A. Harper, in September, 1902 (Herb. Univ. Wisc.).

MEXICO.

On *Pinus* sp. Locality unknown (Herb. N. Y. Bot. Gard.).

On ————————. Locality unknown (as *Polyporus Xalapensis* Berk, *in* Jour. Bot. & Kew Misc. **1**:103, 1849); Jalapa, Chas. L. Smith, January–June, 1894 (Central American Fungi, No. 122); W. A. Murrill, in December, 1909 (Herb. N. Y. Bot. Gard.).

CUBA.

On ————————. Locality unknown (as *Polyporus Flabellum* Mont. *in* Pl. Cell. Cuba, p. 388, pl. 15, f. 2, 1842); (as *Polyporus laceratus* Berk. *in* Ann. Mag. Nat. Hist. **3**:392, 1839, according to Saccardo, Syll. Fung., **6**:231, 1888).

DISTRIBUTION IN SOUTH AMERICA.

BRAZIL:

On ————————. Sao Francisco dos Compos, in Province of Sao Paulo, F. Noack, in 1896–1898 (No. 292), according to Hans and Paul Sydow (1907).

DISTRIBUTION IN EUROPE.

SPAIN:

On ————————. Northern Spain (Herb. N. Y. Bot. Gard.).

FRANCE:

On ————————. Carqueiranne, E. Jahandiez (Herb. C. G. Lloyd, Nos. 09227, 08 + 48, and 11282; New Caledonia (Herb. C. G. Lloyd, No. 0608); locality unknown, N. Patouillard (Herb. C. G. Lloyd, No. 3931).

GERMANY:

On ————————. Dresden, O. Pazschke (Herb. C. G. Lloyd, No. 13101).

AUSTRIA-HUNGARY:

AUSTRIA:

On ————————. Tirolo, Rev. Bresadola (Herb. C. G. Lloyd, No. 3903); Wien, von Höhnel (Herb. C. G. Lloyd, No. 08725).

HUNGARY:

On ————————. Travnik, E. Brandis (Herb. C. G. Lloyd, Nos. 08846, 08847 and 08862).

On *Populus tremula*, *Quercus* sp., and *Tilia* sp. Kmet, in 1891 (Herb. N. Y. Bot. Gard.).

RUSSIA:

On *Betula alba*. Viro B. Eichler (according to Bresadola, Ann. Myc., **1**:76, 1903).

On *Betula* sp. Bialowiezan Lithuania (as *Polyporus simulans* Blonski *in* Hedw., 1888, p. 280, according to Saccardo, Syll. Fung., **9**:185, 1891).

On ————————. Majkop, N. Schustenow (Herb. C. G. Lloyd, No. 1703).

DISTRIBUTION IN ASIA.

JAPAN:

On *Pinus* sp. Settsu, Ch. Tanaka, in August, 1908 (Polyporaceae of Japan, No. 62).

MALAY PENINSULA:

On ————————. Perak (Herb. N. Y. Bot. Gard.).

PHILIPPINE ISLANDS:

LUZON:

On ————————. Lamao Forest Reserve, Bataan Province, H. M. Curran, in July, 1907 (Flora of Philippines, Herb. Bureau of Science).

DISTRIBUTION IN OCEANICA.

AUSTRALIA:

On ————————. Victoria, De Müller (as *Polyporus dispar* Kalchbr. *in* Symb. Myc. Austral., II, n. 82, according to Saccardo, Syll. Fung., **6**:262, 1888); Queensland (according to D. C. McAlpine, Syst. Arr. Austral. Fungi, 1895, pp. 48–49).

Von Schrenk and Spaulding (1909, p. 57) state that they have collected *Polystictus pergamenus* on *Quercus imbricaria* Michx., a species not included among the host species cited

in the above list of exsiccati. Furthermore, Kauffman (1918) reports the sycamore (*Platanus occidentalis* Linn.) as a host for this fungus. From the foregoing data it is evident that the following woods[4] are attacked by *Polyporus pargamenus:*

Pinus virginiana
Tsuga canadensis
Juglans cinerea
Hicoria minima
Hicoria ovata
Hicoria alba
Hicoria glabra
Salix nigra
Salix discolor
Salix lasiandra
Populus tremula
Populus tremuloides
Populus grandidentata
Populus balsamifera
Populus acuminata
Populus trichocarpa
Betula alba
Betula papyrifera
Betula populifolia
Betula occidentalis
Betula lutea
Betula nigra
Alnus incana
Alnus tenuifolia
Carpinus caroliniana
Fagus atropunicea
Castanea dentata
Quercus alba
Quercus garryana
Quercus prinus
Quercus virginiana
Quercus rubra
Quercus texana
Quercus coccinea
Quercus velutina
Quercus californica
Quercus palustris
Quercus marilandica
Quercus nigra
Quercus imbricaria
Quercus phellos
Ulmus americana
Toxylon pomiferum
Liriodendron tulipifera
Persea pubescens
Sassafras sassafras
Liquidambar styraciflua
Platanus occidentalis
Prunus americana
Prunus pennsylvanica
Prunus serotina
Cercis canadensis
Gleditsia triacanthos
Rhus vernix
Ilex opaca
Acer pennsylvanicum
Acer saccharum
Acer saccharinum
Acer rubrum
Tilia americana
Tilia platyphyllos
Nyssa sylvatica
Nyssa aquatica
Rhododendron maximum
Fraxinus americana

The above list of host species is but a meager indication of the commonly known ones. Unfortunately in most of the available collections the host species are either incompletely, or more often not at all, given. A detailed reconnaissance in this and foreign countries should more than double the size of the present list.

[4] The nomenclature used for the trees mentioned in this list is that of George B. Sudworth. (Check list of the forest trees of the United States, their names and ranges. U. S. Dept. Agr., Div. Forestry Bul. 17:144 pp., 1898).

History and Synonomy.

Since its description in 1838, the identity of *Polyporus pargamenus* has been obscured repeatedly owing to the fact that various forms or collections of it have been described as distinct species. Without due regard for the fact that the various morphological characters of one and the same species of fungus are subject to considerable variation, especially when grown under widely different environments in various parts of the world, mycologists often have been misled and have described aberrant or imperfectly developed forms of this plant as new species. Moreover, the various ecological forms of this plant have been published independently as "new species" in former years from three or four European centers of research, each ignoring the existence of the rest. In many cases these brief early descriptions are entirely inadequate and the poorly preserved type plants, when they exist at all, often fail to supplement them sufficiently. Add to this the host of incorrect determinations found in the literature then current, the wholesale assignment of foreign names to plants exclusively American, and the glittering array of species combined under one name in important herbaria, and the reason for the confusion over the status of this plant becomes clear. *Polyporus pargamenus* is generally believed to have been described first by Fries (1838, p. 480) from specimens collected from trunks of pine in arctic North America by the Franklin Expedition. Dr. W. A. Murrill of the New York Botanical Garden, however, who has recently examined the type specimens, has decided that they are a form of *Polyporus abietinus* Fries [*Coriolus*[5] *abietinus* (Dicks.) Quél.].[6] According to Mur-

[5] In keeping with the present day tendency of a few authors to break up the old cumbersome genera, containing a large aggregation of often heterogeneous species, and to regroup the species into smaller groups containing only closely related species, Murrill (1903, p. 93) states that the name "*Polystictus*" is not valid since it is a synonym of *Coltricia* Gray, proposed in 1821. According to Murrill, this removes "*Polystictus*" since it was not used until several years later by Fries (1851). As a result of this discrepancy Murrill (1903, p. 95) has adopted *Coriolus* Quél. as the generic name for the thin coriaceous species of the

rill (1907, p. 27) the true type specimen of this plant came from Mexico and was described by Fries (1838, p. 443) as *Polyporus prolificans* Fr.

In response to the writer's request for enlightenment upon the obscure early history of *Polyporus pargamenus,* Mr. C. G. Lloyd of the Lloyd Library, who has made a careful study of European polyporoid exsiccati, very kindly wrote the following account:

> Fries, who in his early day was limited in his knowledge of foreign species to a scanty few that had drifted into Europe, got a deformed specimen from Mexico which he named *Polyporus prolificans.* It was not proliferous, however, but a malformation -- a monstrosity.
>
> Some years afterwards Klotzsch (who was a German working in Hooker's herbarium) sent Fries some foreign plants numbered, which Fries named for Klotzsch by number. Among others was one supposed to be the plant in question (*Polyporus pargamenus*), which Klotzsch published, but through some transformation of the numbers, either on the part of Fries or Klotzsch, this plant (or a form of *Polyporus abietinus*) was published by Klotzsch, at least as to part. The specimen is not clearly indicated in Hooker's herbarium today, but is indicated from Klotzsch's description. Perhaps, however, it was *Polyporus abietinus.*
>
> Afterwards, when Fries summarized the subject, he proposed *Polyporus pargamenus* on a plant received from Klotzsch, and applied the name to the plant that you have in question. He received the plant from a number of correspondents since, and he always named it as *Polyporus pargamenus,* as evidenced in his herbarium today. *Polyporus pargamenus* came into use not only at Upsala, but throughout the mycological world, for Fries in those days was supposed to know his own species, and those who were in correspondence with Fries, such as Berekeley and Montagne, engaged in naming plants, used Fries' name. There are several hundred specimens in the various museums in Europe and the United States, practically all of them labelled as above. To attempt to change the name at this late date would be absolutely futile, even if it were based on any merit. To take the position that a plant, always called *Polyporus pargamenus* by Fries and every other leading mycologist, be changed to another name and claimed to be on the authority of Fries is absurd on the face of it, and places Fries in a false position.

Polyporaceæ, this name being founded on *Polyporus zonatus* Fr. and seven other species by Quélet (1886), according to Murrill (1906, p. 640).

[6] The close resemblance of these two species, namely *Polyporus pargamenus* Fr. and *Polyporus abietinus* Fr. had lead to considerable confusion in the examination of very old herbarium specimens.

Some years ago Bresadola got a clue to the Klotzschian history, and in one of his papers called the plant "*Polyporus biformis*". It was really based on probable fact but Bresadola only followed it for a short time, for, as every one else who attempts to change established nomenclature for some trivial reason, he has since receded from his position.

In the meantime, however, the plant was found in southern France, where it is an extremely rare plant, and a specimen drifted in to Boudier. The latter submitted it to Patouillard, and he being in touch with Bresadola, gave it the name Bresadola was using at that time. This is the reason why the plant was illustrated in Boudier's "Icones" as *Polyporus biformis*. . . .

There is a strong probability that the Mexican plant which came originally to Fries was but a malformation of this same plant. Fries made two mistakes regarding it: First, in considering that it was a species when it was simply an abortion and should not have been named; and second, in naming it "prolificans" when it was not proliferous, but malformed. Although the plant, through some unfortunate chance, still remains in Fries' herbarium, being one of the very few that have persisted, Fries never recognized it as being the same plant that he got normal specimens of from several correspondents and always called *Polyporus pargamenus*. It seems to me that anyone that substitutes this plant for *Polyporus prolificans* is putting Fries in a ridiculous position if he writes Fries after it, for he is virtually claiming that Fries' blunder should take precedence over his intelligent work. I believe, if Fries were alive today, he would resent it as vigorously as I do. It is unfortunate enough when a man makes a blunder of this kind, but doubly so if it is brought up and paraded years after his death.

As to the question whether the particular specimen sent by Klotzsch to Fries is the plant that you have in question (*Polyporus pargamenus*) or a form of *Polyporus abietinus*, my impression is that the particular specimen from Klotzsch is not preserved in Fries' herbarium. I am sure, however, that there are several specimens that were named *Polyporus pargamenus* and that they are the same plant that you are considering, and if you virtually make the charge that Fries, in addition to not recognizing the old abortion, did not distinguish between *Polyporus pargamenus* and *P. abietinus*, I hardly feel that you will be able to maintain it. . . .

You ask "what will become of Fries' *Polyporus prolificans?*" I think it will remain in a state of "*innocuous desuetude*" as it has remained for nearly one hundred years, and would have remained forever if it had not been dug up as a juggle. . . .

The following list of names may be taken as a partial index to the synonomy of *Polyporus pargamenus:*

Polyporus pargamenus Fries, Epicr. Myc., 480, 1838. (Type from arctic North America.)

Polyporus laceratus Berk., Ann. Mag. Nat. Hist., **3**:392, 1839. (Type from Louisiana.)

Polyporus Flabellum Mont., Pl. Cell. Cuba, 388, pl. 15, f. 2, 1842. (Type from Cuba.)

Polyporus Menandianus Mont., Ann. Sci. Nat., II, **20**:362, 1843. (Type from New York.)

Polyporus subflavus Lév., Ann. Sci. Nat., III, **5**:300, 1846. (Type from New York.)

Polyporus Xalapensis Berk., Jour. Bot. & Kew Misc., **1**:103, 1849. (Type from Mexico.)

Polyporus Sartwellii Berk. & Curt., Grevillea **1**:51, 1872. (Type from New York.)

Polyporus ilicincola Berk. & Curt., Grevillea **1**:52, 1872. (Type from Alabama.)

Polyporus pseudopargamenus Thuem., Myc. Univ., no. 1102, 1878. (Type from New York.)

Coriolus pargamenus (Fr.) Pat., Tax. Hymen., 94, 1900.[7]

Coriolus subchartaceus Murrill, North Am. Fl., **9**:24, 1907. (Type from Colorado.)

Coriolus prolificans (Fr.) Murrill, North Am. Fl., **9**:27, 1907.[8]

Polystictus[9] *pargamenus* (*pergamenus*[10]) of most American authors.

As can be surmised readily from the list of the more important synonyms given above, *Polyporus pargamenus* has had rather a chaotic past history. If we discredit the monstrosity named "*Polyporus prolificans*" by Fries we may consider that Fries' *Polyporus pargamenus*, described originally, under the name in current use, from specimens collected by the Franklin Expedition on trunks of pine in arctic North America, is the type of the species made the subject

[7] Inaccurately cited by Patouillard as "*Coriolus pergamenus* Berk.", and correctly given by Murrill (1906, p. 654).

[8] Based on the monstrosity named "*Polyporus prolificans*" by Fries from specimen from dead deciduous trunk in Mexico.

[9] As stated earlier, the name "Polystictus" is invalid since S. F. Gray in 1821 used "Coltricia" for the plant which Fries made the type of Polystictus in 1851.

[10] This perverted spelling was inaugurated at least as early as 1860. Since its use by Saccardo it has been widely followed by American writers.

of this study. A year later Berkeley described it from New Orleans, La., under the name of *Polyporus laceratus.* Three years after this Montagne described and figured collections of this plant on dead branches and trunks in Cuba as *Polyporus Flabellum.* Types at Paris are well preserved. Then Montagne found it among Menand's New York collections and gave it the name of the collector. Later Léveillé briefly described a form of *Polyporus pargamenus,* collected on trunks in New York by Sallé, as *Polyporus subflavus.* In 1849 Berkeley described collections from Mexico and South Carolina as *Polyporus Xalapensis.* In 1851 Fries erected Polystictus for a section of *Polyporus* as an experiment, changing *Polyporus pargamenus* to *Polystictus pargamenus.* Fries' name is based on *Polystictus parvulus* Kl., a close ally of *P. perennis,* and must therefore stand as a synonym of Coltricia proposed by S. F. Gray in 1821 for *P. perennis* and two other species. Several years afterward Berkeley and Curtis described a poroid form of the plant, collected on trunks in New York by Sartwell, as *Polyporus Sartwellii,* the types now being preserved at Kew. During the same year the same authors described other collections, made by Peters on bark of *Ilex opaca* in Alabama, as *Polyporus ilicincola,* the types at Kew not being well preserved. Later Thümen named a poroid form of the plant in question *Polyporus pseudopargamenus* in contradistinction to the hydnoid form which he considered the real *Polyporus pargamenus.* In 1900 Patouillard adopted the generic name Coriolus, proposed earlier by Quélet, thus making the name *Coriolus pargamenus.* In the case of the splitting of the old cumbersome genus Polyporus and the regrouping of the species into a number of smaller groups containing only closely related species the writer regards "*Coriolus pargamenus*" as the correct name. In 1907 Murrill described a thick poroid form of the plant from the western United States as *Coriolus subchartaceus.* The last name given to this plant is "*Coriolus prolificans,*" based on Murrill's belief that Fries' *Polyporus pargamenus* is synonymous with his *P. abietinus,* and that the monstrosity named *Polyporus*

prolificans by Fries is therefore the type of the plant in question.

The synonomy of this variable plant might be extended considerably. Murrill (1906, p. 655) states that, according to Bresadola, *Polyporus dispar* Kalchbr. and *Polyporus simulans* Blonski should be added for the European forms and that there are probably half a dozen or more from other regions. According to Murrill (l. c.), specimens from North America have been variously determined as *Polyporus elongatus* Berk., described from Manila, *Polyporus nilgheriensis* Mont., described from India, and *Daedalea ferruginea* Schum., described from Denmark.

The Fungus.

Description of the Sporophore.

Technical Description.—Pileus exhibiting great ecological variation, ranging from thin to comparatively thick, tough, corky-leathery, sessile or affixed by a short tubercle, effused-reflexed, imbricate, dimidiate, or flabelliform, frequently becoming laterally confluent, broadly or narrowly attached, often with cuneate base, 1-7 by 1-7 by 0.1–0.8 cm.; *surface* finely villose tomentose, whitish, cremeous, gray, or sometimes brownish-gray with age, usually but not always marked by a few narrow, more or less shining and distinct buff to dark brown zones, frequently becoming more or less concentrically sulcate; *margin* usually very thin, acute, and sterile, sometimes becoming fertile with extreme age, entire to lobed, often splitting radially when thin specimens are dried, fuscous, violaceous, or whitish; *context* white or whitish, fibrous, usually very thin, rarely more than 1 mm. thick; *tubes* 1-5 mm. long, white to discolored within, the mouths whitish to cremeous or often violaceous, especially toward the margin, becoming yellowish to yellowish-brown with age or upon drying, small, angular, irregular, seriate, averaging 3-4 to a mm. in poroid forms, the dissepiments thin and usually becoming irpiciform at an early age, frequently, however, produced at length in the form of very

thin dentate, but becoming lacerate, more or less concentric lamellæ; *spores* smooth, hyaline, cylindric (rod-like in dorsiventral view but allantoid and obliquely apiculate in lateral view), curved, 5-6.5 by 2-2.25 μ; *cystidia* of variable occurrence; when present, conspicuous, hyaline, blunt, and capitate with an incrustation of mineral matter, 15-25 by 4-5 μ; projecting 0-10 μ; *hyphae* of the context hyaline, 3-4 μ in diameter.

Variation Exhibited by the Sporophores of Polyporus Pargamenus.—In the above technical description an attempt has been made to make the descriptive terms somewhat broad and far-reaching — an absolute necessity when describing a species comprising half a dozen more or less distinct forms. The following account of Peck (1880, pp. 36–37) is cited here since it accurately portrays the range of variation assumed by this plant in the eastern United States.

> "*Polyporus pergamenus*, Fr. The typical form of this species, according to the description, has the pileus coriaceo-membranaceous, rigid, tomentose, concentrically sulcate, white; the pores scriately placed, pallescent and produced into very thin dentate plates. Its habitat is said to be pine, and its locality Arctic America. The species, as now understood, proves to be a very common and very variable one and includes several synonyms. In Ravenel's Fungi Car. Exsicc., Fasc. 1, No. 13, *Polyporus laceratus*, Berk., is represented to be a synonym of this species. Dr. Berkeley himself does not give it as a distinct species in his Notices of North America Fungi, though it was founded on specimens from New Orleans, from which we infer that he does not regard it as a good species. According to the description it scarcely differs from *Polyporus elongatus*, Berk., except in its shape and its larger pores. The former difference is of little value for *P. elongatus* is known to vary very much in shape and size. But *P. elongatus*, according to authentic specimens received from Dr. Michener, can scarcely be regarded as anything more than a mere form, or perhaps variety, of *P. pergamenus*. For of this species we have in this State (New York) two prevailing forms. One form has the pileus tomentose, concentrically sulcate and white, and its pores become paler with age and are at length produced or lacerated into thin dentate plates precisely as required by the description. But it differs from the type in general, though not always, having the pileus too thick to be called membranaceous, and in the pores not being seriately placed. These slight differences, however, are of but little account in such a variable plant as ours is known to be, and there can be no doubt that it should be referred to *P. pergamenus*. The other

form, which is more abundant even than the first, is generally thinner and less distinctly tomentose. Indeed, it is sometimes nearly or quite smooth, and it often appears to become smoother with age. Instead of being concentrically sulcate it is generally more or less marked with narrow delicate zones. There are also fine radiating lines or striations which are more perceptible in the smoother specimens. The color is generally grayish pallid or subochraceous. The pores are usually seriately placed, especially toward the margin, and though variable in color they are commonly tinged with purple when fresh and young, as in the preceding form. As in that form also they become paler with age. This is the form recently published under the name *Polyporus pseudopargamenus*, Thum. When the pileus is narrowed toward its base so that its length is greater than its breadth it is *Polyporus elongatus*, Berk. It occurs on a great variety of deciduous trees, but is most frequent on birch, maple, oak and chestnut. The first form is most common on poplar though not limited to it. I have not found either growing on pine. These two forms run into each other by such insensible graduations that it is not possible to draw any satisfactory line of distinction between them, and therefore, the conclusion must be that both are forms of one species, *Polyporus pergamenus*."

Relation of Environmental Factors to the Morphologic Variation of the Sporophores. – All plants, especially fungi, manifest fluctuating variation in all their characters. Such variations are largely, if not entirely dependent upon the environment. Differences in the kind of food elements supplied, due to the occurrence of fungi on a great variety of hosts in different stages of decay will give rise often to sporophores of variable appearance. Changes in the amount of water available and the length of time that an optimum supply remains available are manifested in the resulting form of the sporophores. Variations in the degree of humidity as determined by the growth site or environment, climatic conditions, temperature, etc., are reflected in the variation of size, shape, and other morphological characters of the sporophores. Probably the greatest factor of all, however, is that of the growth position of the sporophores on the substratum. This factor alone is probably responsible for greater variation in the appearance of the sporophores of fungi than all the others combined. Only when we fully realize the importance of environmental factors in influencing the morphology of the sporophores can we appreciate the value of a broader conception of our species of fungi.

Polyporus Pargamenus Fries Versus Polyporus Abietinus Fries.

Unfortunately *Polyporus pargamenus* frequently has been, and still is, confused with its near relative, *Polyporus abietinus*. Many authors state that the former plant is confined entirely to the wood of dicotyledonous trees, while the latter plant is confined entirely to the wood of coniferous trees, and are of the opinion that this fact affords the only constant character by which they can be separated. The writer wishes to make clear that such an impartially drawn distinction may generally, but will not always, separate these two closely related species, since *Polyporus abietinus* sometimes occurs on dicotyledonous woods and *P. pargamenus* sometimes occurs on coniferous species. Weir (1917) mentions the occurrence of small but typical specimens of *Polyporus abietinus* on *Populus trichocarpa* in the Northwest.[11] The writer (1917[1]) has made collections of *Polyporus pargamenus* from dead trunks of hemlock (*Tsuga canadensis*) upon several occasions both in New York and Pennsylvania. On one occasion he observed both plants growing side by side on the same dead hemlock trunk (Plate II). Upon another occasion a dead hemlock was literally covered with sporophores of *Polyporus pargamenus* alone, up to about eight feet above the base (Plate III). In every case where *Polyporus pargamenus* was observed growing on hemlock trunks the macroscopic appearance of the rot produced was indistinguishable from that produced in this wood by *Polyporus abietinus*. Recently the writer (1918) collected specimens of both plants on a dead scrub pine (*Pinus virginiana*) trunk

[11] Freeman (1905, p. 258) states that *Polyporus pargamenus* occurs abundantly on living larch (*Larix laricina*) trees in Minnesota, and gives an illustration (p. 81, fig. 36) of a larch trunk bearing numerous sporophores of what he takes to be this fungus. He states further that there is strong evidence of it having been the cause of the death of numerous larch trees in Minnesota. A careful perusal of Freeman's work, however, shows that he does not distinguish between *Polyporus pargamenus* and *P. abietinus*, so that the case cited undoubtedly refers to *P. abietinus*.

in Maryland. In this case two groups of typical sporophores of *Polyporus pargamenus* had formed from the mycelium developing out of two insect tunnels about two inches apart in the bark. On adjacent portions of the bark were numerous typical sporophores of *Polyporus abietinus*.

Probably one reason for the confusion of these two species may be that while the specimens collected from trunks of pine by the Franklin Expedition in arctic North America have generally been regarded as the type of our present-day *Polyporus pargamenus,* the plant that has gone under this name in the United States is practically always found on the wood of dicotyledonous trees. As Overholts (1915) states, this has led some authors to regard the original *Polyporus pargamenus* as probably a synonym for *P. abietinus*.

As stated earlier, some authors state that *Polyporus pargamenus* and *P. abietinus* can be distinguished only on the basis of knowing whether they occur on coniferous or dicotyledonous hosts. Since the writer's observations, as well as those of others, show that the determination as afforded by knowledge of the host cannot always be relied upon for the separation of these two species, it would seem advisable to consider them as biologic forms of the same species if they cannot be distinguished on the basis of their appearance and structure. To my mind, however, it is easily possible to distinguish, at least arbitrarily, between these two closely related plants by their appearance and structure alone.

Overholts (1915) states that *Polyporus pargamenus* and *Polyporus abietinus* are very closely related and that they are connected by intermediate forms to such an extent that it is difficult to refer some collections to their proper species. However, he finds the usual form of the fructification to be distinct enough. It is his experience that *P. abietinus* is usually much the smaller, is frequently effused-reflexed with a narrow and often laterally continuous pileus, rarely more than two cm. in length, and that the tubes often break up into lamellæ-like plates — a condition which, so far as the writer's knowledge extends, has never been observed in *Polyporus pargamenus*. According to the same author that

species often grows much larger than *P. abietinus,* sometimes attaining a length of 6–7 cm., and is often fan-shaped or cuneate in outline and attached by a narrow, attenuate, sometimes stem-like base, so that the form and size of the sporophore will usually separate it from *P. abietinus.* Other differences may be pointed out as follows: *P. abietinus* lacks the more or less shining, indistinct, buff, to dark-brown zones which are so characteristic of *P. pargamenus.* The sporophores of the latter plant are sometimes concentrically sulcate but rarely prominently so; those of *P. abietinus,* however, are almost invariably concentrically sulcate and frequently very conspicuously so (Plate IV). The pubescence of the pileus of *P. pargamenus* varies from silky to velvety, while that of *P. abietinus* varies from silky-villous to strigose. The pores of *P. abietinus* are larger, more delicate and shallow than those of *P. pargamenus.* In the latter the mouths of the pores almost always become irpiciform at a very early age — in fact almost as soon as they are formed (Plate I); in the former, however, the poroid configuration of the hymenium usually is retained until maturity (Plate IV). Even then they practically never become irpiciform to the same extent that occurs in *P. pargamenus.* The pores of *P. abietinus* are very thin-walled, usually becoming somewhat radiately-lacerate with age. Both species often have a violaceous or lavender tint to the margin of the hymenium, especially on the margins of young pilei. This peculiar coloration is almost always present in *P. abietinus,* occasionally becoming so pronounced in young specimens that the hymenium is indigo. This coloration may or may not be present in *P. pargamenus,* but when present it is rarely so pronounced as that which commonly occurs in *P. abietinus.* The hymenium of the former plant usually is marked by a prominent sterile margin, except in very old specimens; that of the latter rarely has any sterile margin to speak of. In *P. pargamenus* the freshly growing margin of the pileus is silky at first, while in pilei of *P. abietinus* it is usually more or less strigose from the beginning. The microscopic examination of the

two species fails to furnish additional characters for their separation, other than on the occurrence of cystidia. In general it may be stated that in the usual hydnoid form of *P. pargamenus* cystidia are of infrequent occurrence, whereas *P. abietinus* apparently always is characterized by abundant prominent cystidia that are distinctly capitate with minute crystals. The poroid forms of *P. pargamenus*, however, likewise have the same type of cystidia that commonly occur in *P. abietinus*. The spores of both species agree as to their size and shape.

These two species then are to be distinguished definitely only by the combined use of such characters as the form of the pores and the size, shape, and general appearance of the pileus. In most cases they can be separated by their habitat alone. The writer's collecting experience, however, has shown that the latter character is not always enough to separate them. When once the two plants are learned the matter of form and surface characters will usually be sufficient for the identification of the specimens, even if the habitat be unknown.

Morphology of the Sporophore.

Form of the Sporophore.— The sporophores of *Polyporus pargamenus* vary greatly in size and shape, the resupinate forms often covering the whole under side of a log (Plate V). The sporophores, however, usually are pileate. Neuman (1914) states that his largest specimen is about ten cm. wide, five cm. long, and from 2–4 mm. thick. Although the pileus invariably is sessile, the form of the sporophore is variable, depending upon its habitat. When the pilei develop from the base of a tree they usually are narrowly attached by cuneate bases. When the substratum is well above the ground they are more broadly attached. When the sporophores develop from a standing tree or from the upper half of fallen stems they usually become shelving. However, upon one occasion entirely resupinate sporophores were found on the standing dead trunk of a black oak (*Quercus velutina* Lam.), while

a few pileate sporophores were found on adjacent parts of the same trunk. When the sporophores grow out from the lower sides of fallen stems they invariably are more or less resupinate. Those forming on the under sides of fallen stems become effused over the surface of them and develop into resupinate sporophores when the stems lie immediately upon the ground. If the lower surface of the stem is supported just off the ground the sporophores tend to become more or less pileate in time. Those sporophores which develop between the immediate lower surface and the central peripheral portion of fallen stems are effused at first but the subsequent growth assumes a pileate form.

Development of the Sporophore.— In trees having thin bark with numerous lenticels, such as the yellow birch, the mycelium invariably grows out of the lenticels. The mycelium, after growing out of the lenticels as little white tufts, quickly develops into small nodular masses which, when no larger than 1/16 of an inch broad, begin to differentiate into little pilei each with its hymenial surface developing downward. The development of the pores and production of spores begins at this point and continues until the sporophore has attained maturity.

In other trees having a thicker and fissured bark, such as the oaks or maples, the mycelium develops out of the fissures in the bark, frequently filling them first with a white, felty mass. Certain portions of this felty layer of mycelium develop into small nodular masses which quickly elongate into pilei as previously described. On trees and fallen trunks from which large numbers of sphorophores are developing the whole surface frequently becomes covered with a felty layer of mycelium out of which new sporophores develop from time to time. The young sporophores are shallowly poroid at first but normally the pores become lacerate early. Occasionally mature sporophores are found in which the hymenium has a perfectly poroid configuration even at maturity but such cases are of comparatively rare occurrence.

The poroid form of *Polyporus pargamenus* apparently is confined to species of *Populus* and *Salix*. The writer has made collections of this poroid form on *Populus grandidentata* and *P. tremuloides* in Pennsylvania and New York, and has examined numerous specimens of this form on western species of *Populus*. Recently a specimen of the poroid form on *Salix,* collected at Madison, Wisconsin, came to the writer's attention. Since he had never observed this form of the plant on wood of any other genus than *Populus* he was skeptical of the determination since, from the appearance of the accompanying bark and wood, it may have been either *Populus* or *Salix*. Since the wood of these genera can not be distinguished macroscopically the writer made radial microtome sections to study the structure of the medullary rays which afford the chief distinguishing character, the rays of *Salix* being heterogeneous, whereas those of *Populus* are homogeneous. A microscopic examination of the prepared sections showed that the marginal cells of the rays were upright in contrast to the radially elongated or procumbent cells composing the interior of the rays, thus proving the wood to be *Salix* rather than *Populus*. It is evident, therefore, that the poroid form of *Polyporus pargamenus* occurs on both *Populus* and *Salix,* but apparently is confined to these two genera of the family *Salicaceæ*. The writer wishes to have it distinctly understood, however, that, in addition to the poroid form apparently confined to wood of the genera *Populus* and *Salix,* the typical hydnoid form of *Polyporus pargamenus* is also found occasionally on these hosts.

The poroid forms of *Polyporus pargamenus* found in the eastern and middle western United States depart markedly from the typical form of the plant. The upper surface of the sporophores of these forms varies from light to dark gray, depending on the age of the sporophores. It is zonate but lacks the more or less conspicuous multicolored zones which commonly occur in most specimens of *Polyporus pargamenus,* and is more rigid and hirtose than the usual form of the plant. Like the latter, however, it frequently has

violaceous pores, thus indicating the close relationship of these forms. The point of attachment of the poroid forms usually is much broader than that usually seen in *P. pargamenus* and the sporophores frequently spread out over the bark to a considerable extent before shelving out. The sporophores of these poroid forms are also much thicker than those of the usual form of *P. pargamenus,* often being triquetrous in sectional outline. Specimens of the eastern poroid form submitted to Dr. W. A. Murrill were declared to correspond closely with the type of *Polyporus Sartwellii* Berk. and Curt. described from New York, which he studied carefully while at Kew.

In one collection made in Pennsylvania from a dead sapling of *Populus grandidentata* Michx., the majority of the sporophores were exceptionally thick. A close examination showed that the growth of the sporophores had been checked by dessication early in their life, and that they had revived and developed a new hymenial layer which overspread the old one. In most of the sporophores the new growth apparently commenced at the margin of the old pileus and spread over it in all directions, often completely enveloping the old gray pileus in a new mycelial growth (Plate VI). The sections made through these revived pilei presented two definite layers of growth (Plate XII, Fig. 2). The appearance of this section, in view of the two distinct layers of pores, would seem to indicate that this was a perennial sporophore. The two hymenial layers occurred not only in the larger pilei but also in many of the smaller ones, some of which measured less than a quarter of an inch across. While the sectional view of any one of these pilei would seem to indicate that they were perennial, the macroscopic observations on their size, form, color, and rate of growth do not uphold this inference but testify that the occurrence of two hymenial layers in the pilei were merely the result of periodic or seasonal growth. It is therefore evident that the presence of more than one hymenial layer within a pileus does not necessarily indicate that the pileus is perennial, since the two hymenial layers may have been caused by a revival and

continuance of the growth of the pileus. In this particular case it does indicate that the pileus is ecologically adapted to living and developing under xerophytic conditions which often are such as to temporarily arrest all growth of the pileus.

Lloyd (1917) recently has commented on a specimen of this poroid form on *Populus* sent him by Dr. J. R. Weir, as follows:

> "NOTE 536.—*Trametes pergamena*, from James R. Weir, Montana. A thick, trametoid form of *Polystictus pergamenus*. The Fresian system of genera for the large fungi is probably the best, but it is embarrassing when species assume forms that place them in two genera. The common *Polystictus pergamenus* of our Eastern States is our only polyporoid (excepting *P. abietinus*) that has violaceous pores. The Western form found on *Populus trichocarpa* by Mr. Weir, is a thick, rigid plant, but in other features context, large violaceous pores, etc., is that same species. It was recently named *Polystictus subchartaceus*."

The poroid form on species of *Populus* throughout the West is extremely variable and at times looks quite distinct from the poroid form on species of this same genus in the East. As a general rule the western specimens are much thicker than the eastern, often becoming a centimeter or more in thickness. The upper surface usually is hirtose-tomentose and is marked by more or less distinct, often heterogeneously colored, sulcations which are indicative of the periodic increment made by the pileus during its development. The pores, which are at first thick-walled, become thinner-walled and more or less lacerate with age. A part of the western material examined agrees closely in its macroscopic characters with *Coriolus subchartaceus* Murrill, as evidenced by its comparison with a portion of the type collection of this plant which was kindly furnished the writer by Dr. Murrill. The most striking disagreement was in the absence, in the writer's material, of the shrunken blackish margin present in the authentic material. As a matter of fact this shrunken, blackish margin present in the type specimen was undoubtedly caused by the collection of the specimen before the marginal portion had fully matured. The writer therefore considers that, since the blackening of

the margin when bruised is not a constant character, its mention as a general occurrence does not fortify the description but is misleading. With this character thrown out of consideration a portion of the material at the writer's disposal agreed fully with the portion of the type specimen of *Coriolus subchartaceus*. Still other specimens at the writer's disposal, however, departed markedly from the type material of *C. subchartaceus* in that the pilei were laterally elongated and effused, and almost equilaterally triquetrous in sectional outline. At the rear of these pilei the tubes were more or less thin-walled and lacerate, and attained a length of five mm., becoming progressively shorter toward the margin where they remained thick-walled and entire.

The writer has collected similar laterally elongate, triquetrous, thick-walled, poroid forms of *Lenzites sæpiaria* on fallen trunks of lodgepole pine in Montana, and has come to regard such extreme forms as the ecological growth form of these plants in response to xerophytic conditions.

While the poroid form, including its many varieties departs markedly in many respects from the typical hydnoid *Polyporus pargamenus,* it still bears considerable resemblance to it. The hymenial elements are very similar in both forms. In the various poroid forms studied, however, cystidia predominatingly capitate with minute crystals (Fig. 1, p. 50) as described by Overholts (1915), were invariably present; similar cystidia also occur in the typical hydnoid forms of *Polyporus pargamenus*, but usually less abundantly than in the poroid forms.

The usual type of the poroid form of *Polyporus pargamenus* has sufficient morphological characters in common with the well-established hydnoid form of *P. pargamenus* that it has been included with it by practically all mycologists who have worked with it. Moreover the macroscopic characters of the decayed wood are the same in both cases. On the other hand, the differences between these two forms are vastly more pronounced than those between a number of our other closely related accepted species and the poroid form could rightfully be set aside as a distinct species as

has been done in the past, although it seems useless to multiply species. In fact Murrill (1907, p. 24) has described one of the more aberrant western varieties of the poroid form as a distinct species, *Coriolus subchartaceus*. It should not be correct, however, to refer one extreme type of a particular plant to a distinct species and at the same time not have it include all other closely related types of what obviously is the same plant, namely the thinner poroid forms

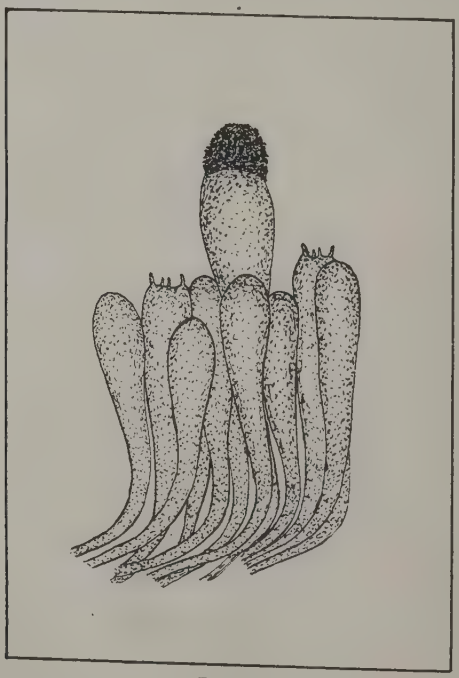

FIG. 1.
Capitate cystidium and basidia of poroid form of *Polyporus pargamenus*, X 2,500.

occurring in the eastern and western United States. In view of the great array of intergrading varieties of this poroid form, the exact status of this form was doubtful in the mind of the writer.[12] Accordingly a number of specimens of the above-mentioned forms were submitted to Mr. C. G. Lloyd, who regards them all as forms of the one species. In Mr. Lloyd's opinion there is nothing in the more obvious variations of the plant nor in the microscopic structure to justify trying to maintain different species where there are so many connecting forms.

Just whether the extremely variable poroid form of *Polyporus pargamenus* is an ecological adaptation, a racial form, or a distinct species, the writer would not like to state in the complete absence of any cross inoculation data. At any rate, among the hundreds of specimens examined by him during the course of this study, few intergradations occur between the poroid form on species of *Populus* and *Salix,* and the typical hydnoid form on the woods of these and other genera. In his opinion the ultimate criterion for making the poroid form a distinct species would be afforded only by the making of cross inoculations. Pure cultures of the poroid form on species of *Populus* and *Salix* should be obtained and inoculated on other species of dicotyledonous woods. At the same time the typical hydnoid form of *Polyporus pargamenus* occurring on these and other species of trees should be inoculated on species of *Populus* and *Salix* and the resulting sporophores compared. The results obtained should show whether this poroid form is a distinct species that may be inoculated and reisolated from various species of trees other than species of *Populus* and *Salix,* or whether it is a biological form aberrant from the type of *Polyporus pargamenus* and arising as a result of some peculiarity of the wood of the species of these two genera that serve as hosts. Furthermore, such an experiment, when conducted under controlled conditions, should determine the

[12] In some of the herbaria examined many of the specimens classified under *Polyporus* (*Coriolus*) *subchartaceus* are merely imperfectly developed or old weathered specimens of *Polyporus hirsutus* on *Populus.*

susceptibility of the sporophores to variation induced by various ecological factors.[13]

In the absence of any cross inoculation data, it has been regarded best for the present to include the poroid forms including both the thick western plant with long tubes on species of *Populus* that has been called *Polyporus* (*Coriolus*) *subchartaceus* by Murrill (1907, p. 21) and the thinner plant with shorter tubes occurring on the wood of *Populus* and *Salix* both in the eastern and western United States under *Polyporus pargamenus.*

The sporophores of *Polyporus pargamenus* grow through only a limited period: When drought or cold weather intervenes, growth is interrupted. However, this and similar tough forms of leathery consistency are able to withstand severe conditions and continue growth after such interruptions so that they are perennial in the sense that they grow from year to year. Growth of the sporophore in this and similar thin, leathery forms is limited mainly to the marginal hyphae and ordinarily the pileus does not increase in thickness. The areas representing the increase in the width of the pileus during the different periods of growth usually are demarked by more or less distinct sulcations. Upon a plentiful supply of moisture, after periods of long drought the pilei frequently renew growth for a time. The result is that one frequently finds specimens that are concentrically sulcate with a broad, bright-colored margin which is in strong contrast to the dark-gray color of the older growth. Each portion of growth does not represent annual growth but does represent periodic growth which took place between periods of drought. This and similar species are said to be annuals in that they do not form more than one layer of pores although exceptions occur occasionally. Growth, however, may begin at any month of the year so long as conditions favorable to growth occur, and continues even during the winter months at intervals when the sporophores are not frozen.

[13] Such an experiment would take at least two, and probably more years' work to complete. For this reason it has not been attempted in the present investigation.

Consistency of the Sporophore.— In the growing margin of the pileus the hyphæ, whatever may have been their earlier arrangement, usually are parallel to one another, little interwoven, and extend in the direction of growth. As the pileus matures they become variously interwoven and modified. In this as well as other coriaceous species the pileus is quite thin and usually fibrous and flexible. Microscopic examination of a pileus of *Polyporus pargamenus* showed that it consists of a mass of branching, sparingly septate hyphæ extending singly or in loose strands parallel to the surface. These hyphæ or strands of hyphæ are but little interwoven and form a tissue homogeneous throughout the pileus. At the upper horizontal surface many hyphæ grow upward and terminate as the hairs of the pileus. Other hyphæ grow vertically downwards and form the trama of the tubes. At maturity the ends of these hyphæ bend outward at right angles and form the elements of the hymenium (Plate VII).

Size of the Hyphæ.— Measurements were made of hyphæ in different portions of the pileus. In different plants of this species the size of the hyphæ is fairly constant, although there may be a slight difference between their size in the different portions of the same pileus. The hyphæ are stouter in the context of the pileus and become smaller in the trama of the pores. Even within the context of the pileus the size of the hyphæ is extremely variable, but they average from 3–4 μ in thickness. The larger hyphæ are very thick-walled and have small lumina. Clamp connections and cross-walls occur but rarely, especially in the larger hyphæ, and then usually are indistinct. In general the size of the hyphæ is of little diagnostic value since there is so small a range of variation in the different species.

Surface Modifications. – The upper surface of the pileus of *Polyporus pargamenus* not only remains incapable of further growth but has a completely undifferentiated surface. The upper surface is composed only of the unmodified terminations of the hyphæ of the context, which end at

the surface singly or in loose strands. The upward extending surface hyphæ become a part of the pileus tissue as growth proceeds and do not differ materially from the hyphæ of the context. The outer hyphæ terminating in many loose ends often give a villous appearance to the surface. Not infrequently minute particles of dirt, bacteria, and occasional spores of other fungi are to be seen among these loosely interwoven ends of the surface hyphæ. Such foreign matter is readily apparent in stained microtome sections. In this and similar forms where no surface growth occurs the exposed hyphæ become darker than those in the tissues below, and, as they become dry, become somewhat appressed. There is no change, however, in the hyphæ themselves or in their arrangement (Plate XII, Fig. 2).

The surface generally is marked by several more or less distinct sulcations. Bayliss (1908), in experiments on *Polystictus versicolor* (L.) Fr., has shown that this sulcation of the pileus is due to an alternate checking and promotion of growth caused by changes in the amount of moisture which, in turn, is dependent upon varying atmospheric conditions. Where pilei were allowed to develop under uniform temperature and moisture conditions hardly any signs of zoning could be observed and the velvety surface, instead of having the usual ribbed appearance, was quite even. The mere changing of conditions of growth so as to secure a drier atmosphere was sufficient to cause a check in the growth and hence a marked zone in the pileus.

The writer observed the natural growth of *Polyporus pargamenus* in the field, making measurements at regular intervals. After a period of drought, during which growth was almost if not entirely arrested, a distinct furrow or zone marked the end of the old zone and the beginning of the new. When the period of drought had been prolonged for a week or more the division line could be seen, in a vertical, radial section through the pileus, extending down to the hymenial surface. When atmospheric conditions were unfavorable to growth the short hairs forming the velvety surface were little or not at all developed. The concentric

sulcations appearing commonly on pilei are indicative of the alternation of decidedly wet and dry periods of growth. The faint zoning which always is present on this and similar rapidly growing, thin pilei are indicative of minor changes in the humidity of the air — in many cases doubtlessly they are due to the check in growth resulting from the fall in temperature which takes place during the night. This is especially apt to be true where we have a succession of cold nights and warm days.

Pilei frequently are found that are exceedingly thin and papery, these being pale-colored with scanty pubescence. On the surfaces of these pilei the zones of growth and bands of color show up very strikingly. In some instances the whole surfaces are shining and have a silky appearance. In general, however, the pilei are much thicker and darker colored; also villous or velvety. Such pilei usually assume a dark-gray or grayish-brown coloration with age and the zones of growth and bands of color are very inconspicuous after the pilei have weathered for a time. Not infrequently one finds both combinations within the same pileus. In this case the grayish, weathered part represents the original growth while recent growth is shown by the lighter colored area that has grown out from the old, dark-colored one, possibly some months after the cessation of growth by the older part.

The biological significance of the velvety hairs which occur on the upper surfaces of the pilei of many species of fungi is a matter of doubt. According to Buller (1909, p. 113) they form a capillary system for the purpose of rapidly disseminating any drops of water which may fall on the pileus. This explanation, while unsubstantiated, at least seems plausible for a drop of water let fall on the dry pileus is absorbed almost instantly by conspicuously hirsute pilei such as *Polyporus abietinus* Fr. and *Polyporus hirsutus* Fr. In more glabrous pilei, for example in sparingly pubescent pilei of *Polyporus pargamenus*, the absorption of water dropped on the surface was much slower. In addition to this the pubescence may be of the same use as is that of

many xerophytic plants. It is generally accepted that the hairs on the leaves of xerophytic plants serve to reduce materially the transpiration. It is therefore reasonable to suppose that the hairy covering protects the sporophores of fungi from rapid dessication. In support of this it may be mentioned that a pileus stripped of its hairy surface dries up far more rapidly than it otherwise would do.

The surface modifications are almost the only differentiations that the tissues of the sporophore undergo. Consequently they should be considered as important characters in any arrangement of the plants on a structural basis.

The Hymenophore.— From a taxonomic point of view the hymenophore is an important part of the fruit body since its poroid character separates the family *Polyporaceæ* from all related families excepting the *Boletaceæ*. The boletes, however, differ from the polypores chiefly in that they are mostly centrally stipitate plants of fleshy consistency and a terrestrial habit, in which the tubes can be separated readily from the pileus in most species. All plants belonging to the *Polyporaceæ,* with few exceptions, have the poroid configuration of the hymenophore — at least in early youth. In *Polyporus pargamenus*, however, which is poroid at first, the dissepiments generally become torn into teeth or lacerate plates soon after the formation of the pores, so that older specimens might easily be mistaken for one of the *Hydnaceæ*.

Development of the Pores.— In *Polyporus pargamenus* the pores are evolved successively from the center or point of attachment outward and are open from the beginning as is the case with the majority of polypores. Such pores are said to be formed exogenously. In the case under consideration they arise directly from a layer of hyphæ differentiated from the trama. A section through the growing margin shows the early stages of pore formation. On the lower side of this portion of the pileus the hyphæ are more closely interwoven and smaller and instead of the hyphæ extending parallel with the surface they are arranged obliquely. In section a few hyphæ can be seen that grow more rapidly than

adjacent hyphæ and extend downward at right angles to those of the surface. These rapidly growing hyphæ extend over the lower surface of the young pileus in the form of a net, the regions in which the hyphæ do not grow corresponding to the meshes and forming the future pores. Basidia begin to appear when the pore cavities are quite shallow. They are formed by some of the hyphæ growing outward at right angles and englarging at the free ends. Consequently the pores at the margin are often immature when those at the rear of the pileus are fully developed. Examination of sections of the sporophores shows that the bases of the pores all lie in the same plane.

Relation of the Hymenophore to the Pileus.— In *Polyporus pargamenus* the hyphæ of the context extend parallel to the surface. When the pores are formed some of the hyphæ or their branches extend obliquely downward, and, turning gradually, soon grow at right angles to the hyphæ of the context. Thus the course taken by the hyphæ of the context extends at right angles to that taken by the hyphæ of the hymenophore. The trama of the pores is no denser than that of the pileus. The hyphæ are slightly finer but then they are not so old as those in the context of the pileus.

The arrangement of the hyphæ in the context of the pileus must determine to a large extent their arrangement in the hymenophore. At least a certain number of the hyphæ must extend in the direction of growth. If, therefore, the hyphæ in the context of the pileus are parallel to the surface as they descend into the hymenophore, they must change their direction to that of the pores which are vertically opposed to the pileus.

The Pore Walls.— Associated with the thickness of the pore partitions or dissepiments are modifications of the edges of the pore openings such as dentations and lacerations. In *Polyporus pargamenus* the pore-walls are very thin. At an early age they become irregularly lacerated and when the slits progress to the base of the cavities the segments appear as hydnoid processes. Such plants can be mistaken easily

for *Hydnum ochraceum* Quél., especially when the walls are thus broken up in the young stages of the sporophore, as is often the case with *Polyporus pargamenus.*

Color.— The color of the pilei of *Polyporus pargamenus* varies greatly in different sporophores, the variation apparently being influenced by the host as well as by other external factors. For example, the writer has noticed and is corroborated in his observation by the experience of Mr. C. G. Lloyd who states that he finds that the most intensely colored sporophores occur on wild cherry. In color there may be all gradations from white, at the beginning of the appearance of the fruit bodies, or in the case of their growth in the absence of light, to gray or brownish-gray with age and weathering. The context of the pilei is uniformly white but usually becomes somewhat discolored with age. In fresh growing specimens the hymenial surface is frequently tinted violaceous, sometimes very strikingly so. This peculiar coloration, however, usually is a transient one.

Either coincident with or within the individual zones of growth there are a number of variously colored zones of all color gradation from buff to brown. While these colored bands are prominent they usually are not so striking as those exhibited by *Polyporus versicolor* (L.) Fries. This color, which to some extent intensifies the zoning, is largely dependent upon the light. Bayliss (1908) has shown that the coloration in *Polyporus* (*Polystictus*) *versicolor* is due to the presence of a diffuse-yellowish pigment, which, on exposure to light, gradually changes into sepia brown granules. When the sporophore first makes its appearance it is always white as is also any new growth which takes place at the margin of the pileus. In *Polyporus versicolor* Bayliss found that after three or four days a pigment is developed in the hairs which cover the upper part of the sporophore, and also in the surface of strands of hyphæ from which these hairs arise. According to the same author these pigment granules cause the hairs and superficial hyphæ to vary from buff to dark brown, according to the intensity

of the light. Sporophores of *Polyporus versicolor* grown by her in the diffused light of the laboratory, under constant conditions of temperature and moisture, were a uniform pale buff color; only rarely was a zone emphasized by a slight deepening of color. The writer has observed frequently that sporophores of *Polyporus pargamenus,* as well as its near relative, *Polyporus versicolor,* that develop out-of-doors on the lower shaded side of a large log for example, or when shaded by other means, invariably have pale buff upper surfaces. In such a case, however, the zonation of the pileus usually is well marked since the variable atmospheric conditions are responded to by variations in the growth of the hairs. The same sporophores, when they are exposed to a greater intensity of light, develop quite normally and the buff color soon changes to a darker brown shade. If growth is checked rather quickly the margin of the last zone of growth, owing to a deficiency in the formation of pigment, is marked by a lighter band. Therefore the pilei formed in summer, when periods of drought are more frequent and growth is arrested suddenly, generally have many brown bands marking these periods. It is only the fairly young zones of a pileus that show these conspicuous colored bands, for ultimately the whole surface assumes the same dark color, thereby obscuring the bands of color. The zonate appearance visible then is due mainly to the differences in texture presented by the velvety ridges and satiny furrows which become even more conspicuous when the pileus, on becoming quite dry, has the well-known gray appearance. A pale buff-colored pileus, when once detached from its host and allowed to dry for some time is incapable of developing the darker pigment when exposed again to ordinary atmospheric conditions.

The Elements of the Hymenium.— The hymenium of *Polyporus pargamenus* apparently consists of but three distinct structures (Plate VII), viz.: (a) colorless basidia, usually with four sterigmata and spores, (b) blunt cystidia capitate at the apex with an incrustation of mineral matter, and (c) a basidium-like element which is asterigmate, usu-

ally shorter, and less enlarged at the tip. The latter element corresponds to what has been termed paraphyses in the Hymenomycetes. According to Curtis (1914) the so-called paraphyses of the Agaricales are nothing more than potential basidia and continue to develop as such during the life of the fungus. It is more reasonable to regard these organs as potential basidia than as inert structures which serve only as reinforcing or spacial agents, as some have viewed them. Owing to the leathery nature of such a fungus as *Polyporus pargamenus* the necessity for special agents or reinforcing structures is precluded. These organs, under favorable conditions, undoubtedly are capable of developing into mature, spore-producing basidia. This view is supported by reason of the fact that spore formation continues for a long period, and careful examination of sporophores of various ages has shown that the spores produced by a basidium mature at approximately the same time. The spores, however, are shed intermittently over long periods, and from this fact it follows that the basidia probably develop successively during moist periods, a circumstance which would account for the continued spore formation. The examination of sections of sporophores developed in a moist chamber likewise gives evidence that the basidia mature successively. This view is further supported by the fact that sporophores sometimes revive and produce a new hymenium the second year due to accelerated growth of certain hyphæ in the hymenial layer.

The basidia are more or less regularly disposed throughout the hymenium. On the enlarged end of each basidium are four minute spine-like sterigmata, each of which bears a basidiospore. Scattered irregularly among the basidia there sometimes occur conspicuous, blunt cystidia usually capitate with an incrustation of mineral matter.

Cystidia may be defined as the more or less conspicuous sterile organs found either in the hymenium or in the subhymenial tissue of various basidiomycetous fungi. They are the modified ends of some of the tramal hyphæ which extend into the hymenial layer and usually project beyond

the layer of basidia with their spores. As Overholts (1915, pp. 684–685) states, in *Polyporus pargamenus* the presence of cystidia is a variable character, and that they are abundant in some specimens but very scarce in others. In such cases he recommends the making of longitudinal sections of the tubes as the cystidia are sometimes more abundant in one part of the tubes than another.

The cystidia resemble the basidia in shape but are considerably larger and longer, sometimes reaching a length of twenty microns and a breadth of six microns, as stated by Overholts (1915, p. 685). They are further characterized by being distinctly capitate — probably with minute crystals of calcium oxalate — although no crystalline structure is visible even under the highest power of the microscope (Fig. 1). These colorless cystidia are rendered very conspicuous by reason of their capitate tips. Sometimes they scarcely extend beyond the basidia, although they usually project sufficiently far that one can distinguish them readily with the low power of the microscope. In the sections examined none of the cystidia projected more than ten microns beyond the sterigmata of the basidia.

Spore Characters.— The sporphores of *Polyporus pargamenus* were found to begin the production of spores even before they measured as much as 1 cm. in either dimension, and to continue to shed viable spores intermittently until old age. When a fresh sporophore is placed on a glass slide or paper the falling spores rapidly accumulate and a plentiful supply is obtained within a few hours. The spores may be seen to best advantage macroscopically on black paper, where the numerous little white heaps look like an imprint of the hymenial surface of the sporophore. Owing to their pronounced adhesiveness they adhere to one another and to any surface with which they come into contact with considerable tenacity. Spore-deposits, therefore, cannot be shaken off paper or glass upon which they have collected. In fact they adhere so tenaciously that, when shed upon glass and dried, they can be scraped off as ribbons 4 or 5 mm. long.

The rate of accumulation of a spore-deposit is dependent upon several factors — for example, age of the pileus, amount of moisture present and the rate of dessication, temperature, etc. By moving a pileus from one place to another every hour and thus securing successive spore prints, one may be convinced readily of the continuity and regularity of the spore discharge. Spores which have just been liberated always have a fresh and turgid appearance and even liberated spores of long standing quickly acquire it upon being placed in water for a few minutes.

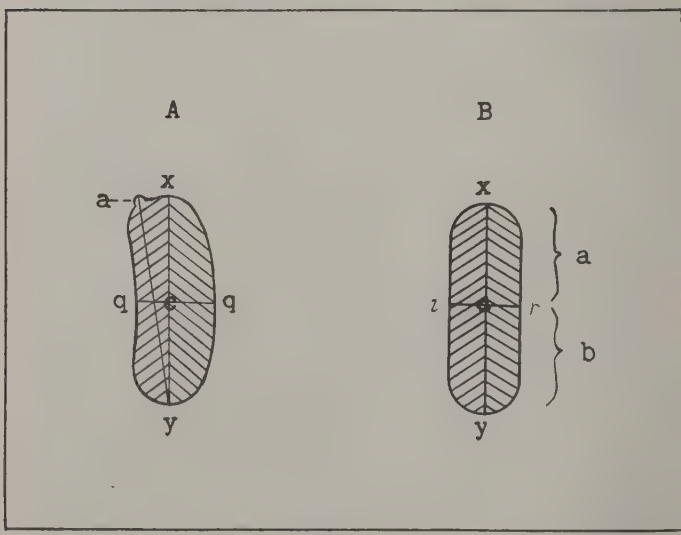

FIG. 2.

Basidiospores of *Polyporus pargamenus* shown in longitudinal section, X 5,000. A. Dorsiventral section, the spore being in lateral position.— *a*, apiculus; *y*, apex; *c*, geometrical center; *ay*, organic axis; *xy*, geometrical axis; *qq*, organic section; , ventral spore-half; , dorsal spore-half. B. Bilateral section, the spore-half being in ventral position. *a*, apical spore-half; *b*, basal spore-half; *c*, geometrical center; *xy*, geometrical axis; , left lateral spore-half; , right lateral spore-half. This section represents the only symmetry plane possessed by the spore.

Microscopic examination shows each spore to be a colorless, unicellular body measuring 5–6.5 microns long by 2–2.25 microns broad, the protoplasmic contents of which are homogeneous and usually devoid of vacuoles. In the spores of *Polyporus pargamenus* we distinguish first a base (Fig. 2, A), the point at which the spores are attached to the sterigmata and at which their abcission occurs at maturity.[14] The organic center of the base is the apiculus (a), which is usually situated excentrically and as a general rule does not coincide with the geometric center (x). The organic center of the top is the apex (y), which coincides with the geometric center. The line (ay) which joins the apiculus with the apex is the organic spore-axis. The line (xy) which joins the geometric center of the base with the apex is the geometric spore-axis. The symmetry plane (qq) running transversely through the spore at the central point (c) of the geometric axis is to be regarded as the spore cross-section.

As seen from the base and apex, every basidiospore is oriented in a definite manner, and we distinguish therefore four surfaces: a dorsal and a ventral side as well as a right and left lateral surface. The spores on their basidia are directed with their dorsal surfaces toward the outside and with their ventral surfaces toward the inside, while they limit one another laterally with a side surface. The dorsal and ventral sides are divisible into two symmetrical surfaces by a basipetally running symmetry line (Fig. 2, B) (xy). The plane formed by the union of the dorsal and ventral sides is the bilateral symmetry plane which divides the spore accordingly into two symmetrical halves, a left lateral (l) and a right lateral (r) part. This is the only symmetry plane always possessed by each basidiospore.

A plane running through the geometric center at right angles to the bilateral section between the dorsal and ventral sides, the dorsiventral section (Fig. 2, A) (xy), divides the spore into a dorsal and a ventral spore half which are never

[14] The form of the geometrical description of the basidiospores is based upon that given by Falck (1909, pp. 76–79) for the spores of species of Lenzites.

perfectly symmetrical. If we see the basidiospore from the dorsal or ventral sides (Fig. 2, B) in the outline of the dorsiventral section we denote its position and its cross-diameter as dorsiventral (either dorsal or ventral); on the contrary, if the side surface is turned to us we see it in the contour of the bilateral section (A) and we denote its position as lateral (either left or right).

The spore cross-section lying at right angles to the bilateral and dorsiventral section (B, lr) divides the spore into two more or less unequal halves, a basal half (a) with the apiculus and an apical half (b). If these two halves as seen from the apiculus and the apex (also observed from the dorsal side) are shaped alike or approximately alike we denote the basidiospore as being basally equally halved, in other cases as basally unequally halved. If we see the spore from above or below in the outline of the cross-section we denote these positions respectively as the apical and basal views and the diameter of the cross-section as the basipetal diameter. These symmetry proportions, which correspond with the definite spacial orientation of each individual spore, are possessed by the spores of all Basidiomycetes.

In the microscopic examination the spores of *Polyporus pargamenus* appear according to their positions in a given view. In general we see them in the lateral view with the contour of the bilateral plane (Fig. 3, l and r). In this sidewise position the spores have the form of a small kidney. We distinguish accordingly a convex dorsal side and a concave ventral side. According to the position of the apiculus we can distinguish a left (l) and a right (r) lateral position. Moreover, the various lateral deviations from the sidewise position are to be judged according to the orientation of the apiculus.

In both the dorsal and ventral positions we see the spores in the contour of the dorsiventral section as symmetrically formed, straight rods with both ends rounded (Fig. 3, v and d). By vertical orientation of the spore with the apiculus above we may determine whether the dorsal side lies toward one. The more the spore is shifted from the dorsal

or ventral side to the lateral position, just so much the more does it approach the exact symmetry of the allantoid form, while the apiculus changes again to the lateral position.

The transverse diameter of the spore remains approximately the same in the different changes of the indicated positions; at least no noticeable differences could be detected with the measuring devices at my disposal. Therefore it may be inferred that the cross-section (basipetal view) must exhibit an approximately circular contour, which can be corroborated by direct microscopic examination from above or below (Fig. 3, q).

The spores consequently are basipetally bilateral in transverse section; in longitudinal section they are bilaterally symmetrical dorsiventrally and strongly unequally halved laterally. They appear colorless by transmitted light and white by reflected light.

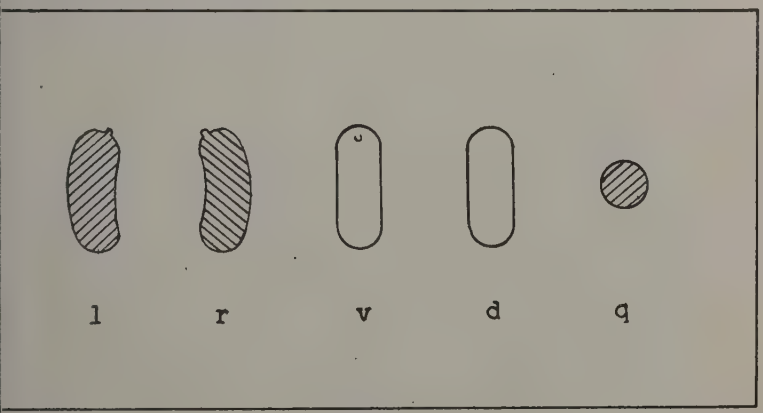

FIG. 3.

sidiospores of *Polyporus pargamenus* in different positions, X 3,000. *l*, left lateral the apiculus lying to the right side; *r*, right lateral view, the apiculus lying to the side; *v*, ventral view, the apiculus lying in the symmetry plane; *d*, dorsal view, the ulus not being visible in this view; *q*, transverse section at the central elevation.

Germination of the Spores.

Methods.— Spores were obtained in most cases from sporophores (dessicated or otherwise) gathered as needed from a nearby tree. The sporophores on this particular tree remained in a state of dessication throughout the winter, so that spores could be obtained whenever needed. In some instances dessicated sporophores were stored in the laboratory and revived at will by soaking in sterile distilled water, after which they were placed in sterile petri dishes. In this way the spore prints were obtained on sterile glass plates. The germination tests were made in the usual way in van Tieghem cells, using various nutrient media. All cultures were made in the laboratory at ordinary room temperatures. It was found that germination of the spores took place readily in any medium that was reasonably suitable for fungous growth. As a general rule a few spores invariably germinated after eighteen hours' time. Occasionally a few spores germinated as early as sixteen hours after their introduction into the hanging drop culture. In general, at the end of twenty-four hours the majority of the spores were germinated. Temperature seemed to be the main factor governing the time required for germination. The presence or absence of light made no perceptible difference in the length of time required for germination. The effect of direct sunlight, however, which Buller (1909) showed to retard the germination of spores of *Schizophyllum commune* Fr., was not tried. The use of different culture media did not have any marked effect upon the interval of time between the introduction of the spores into the hanging drop and the first signs of germination. The percentage and regularity of germination, however, was directly proportional to the suitability of the culture medium used. The germination of the spores, of course, was studied in the more favorable culture media.

Description of Germination.— Germination was found to occur generally, although by no means always, at the apiculate end of the spore. Almost always a single germ tube is

put out at one end of the spore and very shortly after this another one is put out from the other end. Occasionally germ tubes are put out simultaneously from both ends, but in general one seems to precede the other. In some instances, however, the one germ tube makes considerable growth before the spore puts out one from the other end. Germination from the side of the spore is of rare occurrence.

No instances were observed in which more than two germ tubes were put forth from a single spore. The spores were not observed to become vacuolate before germination, although spores which failed to germinate became 2-vacuolate and more or less distorted after lying in the hanging drop culture for a few days. After several days they were found to have collapsed. Even after several weeks the collapsed spores could be clearly detected in the drop. Before putting forth germ tubes the spores swelled up to less than twice their original size. The germ tubes are nearly as wide as the spores and germination seems to be merely a gradually tapering prolongation of the spore wall. After a few days' growth it was usually impossible to distinguish the position of the original spore wall in the mycelium. In many instances, especially in slowly growing plants, small globular inflations or cysts were noticed on the mycelium, some being lateral and others terminal (Plate VIII, h; and Plate IX, 2, 3, 4, and 5). These local enlargements of the hyphæ evidently were peculiar to this particular fungus for they were observed to occur after forty hours' growth in a number of hanging drop cultures in practically every medium used in which germination was secured. No such abnormality, however, could be detected in any of the numerous cultures made on solid media.

It was clearly evident that these peculiar cyst-like bodies were not reproductive bodies. It is the writer's opinion that they occur solely as a result of the physiological response of the mycelium to the excessively unnatural conditions of the nutrient medium for its growth. The mycelium invariably developed large numbers of these globular enlargements in the younger stages of its growth, but ceased to develop them

and became more regular and constant in its growth as it grew older. Such a physiological response of the mycelium is not phenomenal, since the mycelium of the fungi in general must necessarily be very plastic and susceptible to response in order to more nearly bring it into harmony with the extremely varied conditions under which it must grow.

In those hanging drop cultures in which the growth of the mycelium seemed to have come to a standstill, due probably to lack of sufficient nutriment for further growth, it was noticed that the mycelium invariably became strongly vacuolate. In hanging drop cultures of basidiospores grown in sugar-wood decoction it was observed that the mycelium, after two weeks' growth, began to break up into oidia.

The germ tubes develop rapidly into an extensive primary mycelium characterized by the total absence of clamp connections and the rare occurrence of cross-walls. In thriving cultures the mycelium branches profusely soon after the germination of the spore. After five or six days[15] the hyphæ of the primary mycelium give off branches which differ from those of the primary mycelium in that they possess abundant clamp connections and cross-walls. These hyphæ constitute the secondary or mature mycelium which at first grows interningled with the primary mycelium and sometimes anastomoses with it. The latter, however, soon loses its contents and disappears from the culture. This change in the mycelium occurs regularly in all cultures, both those in hanging drops and those on agar plates, and apparently is not influenced by the nature of the culture medium or by other external conditions.

The germination of the spores and the method of growth of the mycelium is illustrated by camera lucida drawings on Plates VIII and IX. In connection with each of these plates the age of each germinated spore is indicated approximately. The size attained by the mycelium varies greatly according to the suitability of the culture medium used and the conditions for growth. In general the drawings represent the

[15] Usually longer in hanging drop cultures.

maximum growth obtained in the indicated time with the best media used.

Culture Media Used and Results Obtained.— Spores germinated as quickly in both distilled and tap water as they did in the nutrient media used. Germination in distilled or tap water was by no means so abundant and the growth of the mycelium was by no means so great as was obtained by the use of suitable nutrient media. It was surprising to find that one spore germinated in distilled water attained a length of 315 microns. Its subsequent growth, however, was not followed farther. The spores, whenever tried, exhibited more or less germination in distilled water. It is evident that an external food supply is not necessary for germination of the spores of this species, although it greatly accelerates the power of germination and serves to sustain subsequent growth.

A good culture medium for the germination of spores in hanging drop cultures was made up as follows: Finely divided basswood (any other dicotyledonous wood may be substituted) to the extent of 15 gms. was boiled in tap water, the extract filtered, and water added until it measured 200 cc. To this filtered extract was added 200 cc. of a 2 per cent solution of cane sugar and the resulting mixture was tubed in small quantities and sterilized. An even better culture medium consisted of a 3 to 5 per cent solution of Merck's malt extract.

A number of germination experiments were performed, using many unusual substances largely out of curiosity to see how resistant the spores would be to adverse conditions. It has been reported frequently that the germination of spores was stimulated by slight quantities of ether or alcohol, but such did not prove to be the case with spores of *Polyporus pargamenus*.

Germination in a 0.5 per cent solution of ether was greatly retarded and only rarely was it observed even after eighteen hours. The mycelium from the few spores that germinated apparently grew well for about two days, but soon became extremely vacuolate and formed numerous

globose swellings. Ungerminated spores usually became 2-vacuolate. Germination in 0.5 per cent ethyl alcohol was greatly retarded — even more so than by the use of ether — and confined entirely to a few spores. Subsequent growth and behavior of the mycelium was the same as described for the use of ether. Germination in a 0.5 per cent solution of dipotassium phosphate was retarded to about the same extent as by alcohol, but occasional germination was to be seen. The growth of the mycelium was poor and highly irregular. After the escape of the protoplasm from the spore, through the germ tubes, it was noticed in a few instances that a cross wall was formed through the center of each spore. Spores germinated and grew vigorously in a 0.5 per cent solution of sodium chloride (Plate X). No germination could be observed in the following solutions: 0.5 per cent potassium nitrate, 1.0 per cent tartaric acid, 1.0 per cent ammonium phosphate, 1.0 per cent sodium carbonate, and 1.0 per cent citric acid.

Vitality of Dessicated Spores.—A plentiful supply of spores was shed on waxed paper and the paper was folded up and filed away in a desk on November 8, 1915. It was found that these spores germinated readily after being kept in this condition for two weeks and it seemed desirable to obtain data on the duration of vitality of dessicated spores. As a result of germination tests made at various intervals from these spores, using hanging drops containing a 5 per cent solution of Merck's malt extract, they were found to germinate as readily at the end of six months as when first shed. The growth of the mycelium, however, was very rapid and profuse branching occurred. The spores were again tested at intervals and were found to germinate readily at the end of ten months. Further tests were not made until twelve months had elapsed since the spores were shed. At this time several tests for germination all resulted in failure. The dessicated spores swelled up in the nutrient solution as they had done before, but not a single case of germination was observed.

It is remarkable that such minutely microscopic plant structures as these fungous spores should retain their vitality, germinate, and develop into infectious plants after being kept for ten months in the state of extreme dessication afforded by their storage in a warm room. That these results are not out of accord with the vitality of the spores of other wood-destroying fungi are shown by the experiments of Falck. Falck (1909) succeeded in germinating spores of species of *Lenzites,* some of which had been preserved in a state of dessication on glass slides for one year and nine months. He found that in general the spores of *Lenzites* species retained their vitality longest when they were collected in thick layers on dry glass slides and carefully preserved dry. When the spores became wet by the moisture expelled from the fruit-bodies in the process of shedding, Falck found that they stuck together and died in a proportionately shorter time. If the waxed paper containing the shed spores of *Polyporus pargamenus* had been stored in some cool place or out of doors it is quite likely that they would have retained their vitality for a considerably longer period than when stored in a warm room. Under natural conditions it stands to reason that the shed spores may be blown hither and thither for weeks and months without losing their vitality. As a result of their ability to retain their vitality after being subjected to dessication for long periods, their chances for becoming lodged in favorable situations are greatly enhanced.

Characteristics of the Mycelium in Pure Cultures.

Culture Methods.—The basidiospore was employed as the source for most of the cultures used in the present investigation. Owing to the thin leathery nature of the sporophores, they are not well adapted to the making of pure cultures by the tissue method. Furthermore, in securing pure cultures from very thin, leathery sporophores one is almost obliged to use the spore method since it is usually very difficult to obtain pieces of uncontaminated tissue from such thin sporophores. In addition it was found to be very difficult to

transfer bits of rotten wood to agar plates and secure a continuation of the growth of the mycelium, since under the increased moisture content of the new environment the mycelium usually became sodden and died. Without regard for the ease with which pure cultures can be obtained from basidiospores, the basidiospore was regarded as the most logical point to begin the culture study, since the possibility of error would be less than if the culture was obtained in some other way, and it was thought that the young mycelium arising from the basidiospore might possess properties and means of reproduction not seen in the more mature stages of the fungus.

To obtain the basidiospores, fresh sporophores of the fungus were collected in the field, wrapped in waxed paper, and brought into the laboratory. The sporophores were rinsed in sterile distilled water, which served not only to remove some of the bacteria and spores of foreign fungi, but also to thoroughly saturate the sporophores. The sporophores were removed with sterile forceps and the excess water was sponged off with bibulous paper which had been previously sterilized, and were then placed, hymenium downward, in large, dry, sterile petri dishes. As Zeller (1916, p. 442) has pointed out, the moisture in the sporophores serves two purposes other than reviving the tissues, in that it keeps the air in the dish sufficiently humid to prevent too rapid dessication, and it also tends to retain foreign spores on the surface of the sporophore, the latter being beneficial in securing a fairly pure dispersion of spores. After twenty-four hours the sporophores had discharged enough spores to make a white spore print.

Where the ungerminated spores were inoculated directly upon poured agar plates, the spore dispersion was made in sterile distilled water. Several loopfuls of sterile water were transferred to the spore print by means of a platinum loop. By stirring a little with the loop the spores were so dispersed that when a loopful was transferred to the center of a poured agar plate it produced a cloudy drop. Where the spores were previously germinated in hanging drop cultures so that their

germination could be observed the spore dispersion was made in the same way except that a number of loopfuls of the spore dispersion were transferred to a blank of the sterile nutrient medium in a test tube which was well shaken by rolling between the palms of the hands. Two or three loopfuls of this diluted spore dispersion were transferred to the cover glasses of sterile van Tieghem cells prepared in the usual way and these were sealed. The germination studies were performed entirely from cultures made in van Tieghem cells. In some cases a platinum loopful of germinated spores was transferred from the van Tieghem cells to poured agar plates as was done in the case of the ungerminated basidiospores. In both cases characteristic colonies were produced on the agar plates, the tufted growth of the mycelium of course appearing on the plates sooner where germinated basidiospores were employed.

Description of Cultures.— Both spores germinated first in hanging drops and ungerminated spores, when transferred to poured plates of prune or malt extract agar, developed into a little tuft of mycelium which gradually spread out over the surface of the plate, making a floccose tuft of mycelium. In some cases the floccose growth of mycelium continued (Plate XI, Fig. 1), while in others, where the mycelium grew under apparently the same external conditions except that a richer culture medium may have been employed, it was found to be breaking up into oidia four days after the inoculation of the spores on the plates. In general it may be stated that when basidiospores were inoculated upon the agar plates there was a tendency for filamentous vegetative mycelium to result (Plate XI, Fig. 1). In some cases, however, the filamentous vegetative mycelium gave way to mycelium that continued to break up into oidia. On the other hand, oidia (both ungerminated and those previously germinated), when inoculated on agar plates, instead of producing filamentous vegetative mycelium always produced mycelium that continued to break up into oidia. (Plate XI, Fig. 2, and Plate XVIII, Fig. 1.)

In the case of attempts to infect sterile blocks of wood b inoculation with spores, both germinated and ungerminated it was noticed that the resulting infection and spread of th mycelium was either very slow or failed altogether. Evi dently there are some conditions for the ready developmen and spread of the mycelium in wood under natural environ ment that are difficult to duplicate by artificial means Otherwise wood would not be attacked so readily in nature A far easier and more reliable means of infecting blocks o wood was found in the method of placing in contact wit them a piece of decayed wood containing active mycelium Upon examination of some successful infections, at the begin ning of the appearance of the mycelium, it was found tha the mycelium had partially broken up into oidia before an considerable mycelial growth had been made. Learn (1912 p. 544) observed that oidia were present in cultures o *Pleurotus ostreatus* Jacqu. on blocks of wood and that nev growths arose at the base of these blocks, apparently due t the shedding of the oidia from above. It is not improbabl that in nature the formation of this secondary spore form may be a useful and additional means of propagation.

The growth of the mycelium on inoculated blocks of steril wood always gave uniform results. In both methods o inoculation (by the use of germinated basidiospores and b contact inoculation by pieces of infected wood) the mycelium spread over the surface of the wood in the form of irregularly running, white mycelial strands of varying thickness (Plate XII, Fig. 1.) A microscopic examination of thes strands showed that they were composed of smaller strand of hyphæ which had anastomosed irregularly to form th larger strands. The smaller strands of hyphæ were com posed of varying numbers of colorless hyphæ which wer fused together in a highly irregular manner. The individua hyphæ exhibited a large number of cross-walls and clam connections and innumerable branching of an exceedingl irregular character. As the strands of hyphæ spread over th surface of the blocks, they gave rise to more or less rounde compact masses of mycelium (Plate XII, Fig. 1), but th

strand formation persisted for a long time. Two blocks (1 x 1 x 4 inches) of the sapwood of sugar maple (*Acer saccharum* Marsh.), inoculated with germinated spores of *Polyporus pargamenus*, exhibited but very little evidence of decay even after six months. A similar block of yellow birch (*Betula lutea* Michx. f.) wood, inoculated by placing a piece of decayed wood in contact with it and keeping it in a culture tube plugged with cotton wool, exhibited considerable decay in this period.

Very successful cultures on wood were obtained by making inoculations on a larger scale, using fresh sapwood. A living yellow birch sapling about two inches in diameter was cut up into two-inch blocks, and these were split up into quarters, leaving the bark attached to the wood. A dozen of these blocks were placed in a large Erlenmeyer flask and sterilized under high pressure. After the sterilization the blocks were inoculated with a piece of the inner bark of yellow birch containing actively growing mycelium, the latter having been cultured in a moist chamber for some time previous. The mycelium from this fragment of bark soon spread to the blocks of wood and rapidly attacked the inner bark of these. The mycelium that began to spread over the surface of the blocks exhibited the characteristic strand formation. In the course of a month or so, the mycelium had completely covered the mass of blocks, filling up the spaces between them, and obscuring the strand formation.

The culture was kept on a shelf in the laboratory but was not exposed to the action of sunlight. It was retained for seventeen months, but appeared no different at the end of this time than it did one month after the inoculation was made, and never during this period did it exhibit any signs of sporophore formation. At this time the writer left Syracuse, but sent for the flask two months later. When it was unpacked he was agreeably surprised to find that several abortive sporophores had formed at the margin of the flask where the mycelium had grown part way up the side. (Plate XIII.) These abortive sporophores consisted of small resupinate, hydnoid hymenia, all of which were characterized by

the lack of a context and by the flattening of the teeth as in *Irpex*. In some cases where the mycelium had grown part way up the side of the flask the abortive sporophores had grown out from their points of attachment and formed a few flattened teeth projecting downward as do the pores of normal sporophores. No normal sporophores possessing a context were ever produced in artificial culture.

An effort was made to determine spore production. A sterile coverslip was lowered into the flask by means of a platinum loop fused into a long glass rod, and placed under one of the abortive sporophores. On the following day the coverslip was withdrawn and mounted on a slide on which a drop of water had been placed. A microscopic examination revealed thousands of basidiospores, all of those examined having the characteristic shape and size of the spores of *Polyporus pargamenus*. These abortive sporophores continued to shed basidiospores for several days, the spores tested being viable and germinating in the characteristic manner for the basidiospores of *Polyporus pargamenus*.

It may be that the formation of sporophores previous to the time noted was retarded by the lack of an adequate supply of moisture within the flask since there was very little free water in the bottom of the flask when the experiment was started and none was introduced during the succeeding eighteen months that the experiment was conducted. Upon examination the blocks of wood were found to be soft and spongy, and to have the same pocket type of decay characteristic of yellow birch wood when decayed by *Polyporus pargamenus* under normal conditions.

The Vegetative Mycelium.— Two periods are clearly discernible in the development of the mycelium of *Polyporus pargamenus*, and the mycelium produced in these two periods will be designated respectively as primary and secondary mycelium. The primary mycelium is the product of the germination of the basidiospore and is distinguished by the absence of clamp connections. The hyphæ of the primary mycelium soon lose their protoplasm and disappear. The secondary mycelium arises from the primary in a few days

as a direct outgrowth of the latter; it is composed of hyphæ of normal size that bear numerous clamp connections. In *Polyporus pargamenus* the clamp connections form as lateral outgrowths of one cell fusing with the cell beneath it, the separating wall sometimes being formed before the clamp has fused with the next cell (Plate XIV, Fig. I). The secondary mycelial system consists of an intricately branched network of hyphæ comprising both large hyphæ with distinct thin walls, and hyphæ of smaller diameter, formed by the repeated branching of the larger ones; these hyphæ in turn branch and rebranch. At certain points along the larger hyphæ short branches are given off which divide very rapidly into the finest threads which penetrate the cells in all directions. Connections between adjacent hyphæ occur frequently; also rhizomorph-like masses where large numbers of hyphæ have fused together more or less. The latter occur most abundantly in the vegetative mycelium growing over the surface of blocks of wood.

Polymorphism. — Lyman (1907, p. 127) defines the basidiospore, borne on the basidium which is the characteristic organ of the group, as the primary reproductive body of the Basidiomycetes, and denotes all other spore forms, that is, those not borne on basidia, as secondary spores. According to Lyman (*l. c.*) the secondary spores thus far known to belong to species of Basidiomycetes are of four types: (a) chlamydospores — encysted vegetative cells; (b) oidia — the dissociated cells of vegetative hyphæ; (c) budding cells — produced by a yeast-like growth; and (d) conidia — exogenously abjointed cells which show more uniformity of size and shape than do the other types of spores mentioned, and are produced on more or less specialized structures called conidiophores.

Oidia. In the cultures of *Polyporus pargamenus* the division of the hyphæ into oidia was preceded by a contraction of the protoplasm, leaving empty hyphal walls at numerous points along the filament. Later the hyphæ become divided into many short cylindrical cells with rounded ends,

these cells being retained for a time within the walls of the original hyphal filament. If such a filament is mounted dry on a glass slide and viewed through the microscope, the empty membranes between the oidia appear to have collapsed as shown in Plate XIV, Fig. 2, a. At a still later period, the divided filament disintegrates, setting free cells with rounded ends of all shapes and sizes (Plate XIV, Fig. 2, b), most of them being short cylindric bodies varying from 7–25 μ in length and possessing dense refractive contents. In the formation of oidia, both the primary and secondary types of mycelium are equally active, although the oidia usually are not formed directly from the hyphæ provided with clamp connections, but from smaller branches of the size and appearance of the primary hyphæ. The retention of vitality by this secondary spore form was not tested as was done with the primary spores — the basidiospores. [illegible] 1907, p. 149), however, states that the [illegible] vitality by oidia is short, and it is reasonable to suppose that these asexual spores are of less vitality than the basidiospores which probably are of sexual origin.

Recently formed oidia of *Polyporus pargamenus* were found to germinate readily upon being transferred to hanging drop cultures. The germination of the oidia was followed in as much detail as was that of the basidiospores. Oidia transferred from pure cultures on agar plates to hanging drop cells containing sugar-wood decoction were found to germinate in about the same time required for the basidiospores, and always in less than twenty-four hours. Most of the oidia germinated at first from one end only; occasionally, however, germ tubes were put forth simultaneously from both ends. In case only a single germ tube was put forth, a second one was later put forth from the remaining end, although it did not follow as quickly as was the case in the basidiospores, and usually there was considerable growth of mycelium before germination occurred from the other end. Three successive generations of oidia were secured in hanging drop cultures by isolating the oidia when formed and transferring them to new hanging drop cells. Evidently the process of

idia formation can continue indefinitely. Upon germination, the oidia produce mycelium of the primary type, that , mycelium lacking clamp connections (Plate XV and XVI). Falck (1902) cultivated a considerable number of ie *Agaricaceæ* through the formation of oidia to the mature ructification and concluded that the oidium form is a defiite stage in the life-cycle of many of the higher fungi. yman (1907) shows that the production of oidia appears be confined almost entirely to the higher families of the ymenomycetes, as was indicated by Brefeld (1889).

Chlamydospores.— The formation of chlamydospores in *olyporus pargamenus* agrees with the process in other roups of fungi. Any cell of the mycelium, under certain onditions, may form a chlamydospore; hence their position either terminal or intercalary. Cross-walls are not abunant in the vegetative mycelium of *Polyporus pargamenus* nd chlamydospores are of only occasional occurrence. They ay be formed either on superficial hyphæ or on hyphæ that ave become submerged under the surface of the agar. In ie process of their formation the protoplasm of the hypha comes vacuolate, certain cells losing their contents entirely, hile in others which are to produce chlamydospores the ondensing protoplasm contracts away from the ends of the ll and concentrates in the middle region where the side alls become greatly distended to receive it (Plate XVII). ere a resistant wall (endospore) forms about the encysting ll within and adnate to the surrounding hypal walls, and uts off the empty portion of the parent cell at each end. ontinued contraction of the protoplasm may cause the andonment of these end walls, and new walls may form rther in (Plate XVII, c). The mature chlamydospore is ick-walled with dense, granular, refractive contents which come vacuolate with age. As a general rule the terminal lamydospores are pyriform while the intercalary ones are ore or less lemon-shaped, but great variation is exhibited ring to the different degrees of contraction of the protoasm. The mature spores are freed only by the decay of

the empty portion of the parent hyphæ, and are able to withstand adverse conditions for a considerable period. Their germination was not followed. No chlamydospores were observed upon the primary mycelium, all those observed occurring upon the secondary type of mycelium. Oidia and chlamydospores were the only secondary spore forms encountered in the cultures of *Polyporus pargamenus* and it is believed that the occurrence of these additional spore forms in connection with the life history of this plant is reported for the first time.

In a number of cultures coiled or helicoid hyphal formations were of common occurrence. They were observed both

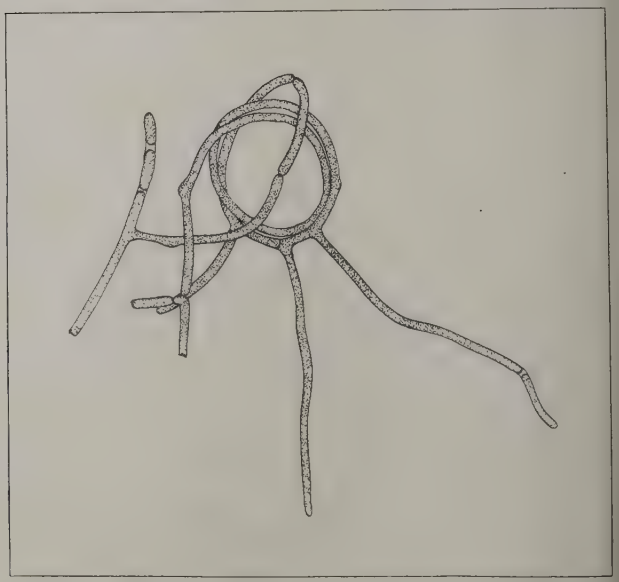

FIG. 4.

Helicoid hyphal formation from agar plate culture of *Polyporus pargamenus*, X 1,000.

in hanging drop cultures where a solution of malt extract was employed for the nutrient medium, and in cultures made on poured plates of malt extract agar. In the former case they were observed in cultures made for the purpose of testing the vitality of shed basidiospores that had been kept in a state of dessication for four months. In the latter case the same formations were found in abundance on the submerged mycelium growing on plates of malt extract agar. In both cases they were associated with mycelium that was breaking up into oidia and the one illustrated in Figure 4 depicts the mycelium breaking up into oidia. Nor particular significance could be attached to these helicoid hyphal formations. Similar hyphal formations have since been seen by the writer on agar plate cultures of Pythium and other fungi.

A portion of a culture on malt extract agar in which the mycelium was breaking up into oidia was transferred to another plate of the same medium. In the course of the next four weeks the developing mycelium spread over the surface of the agar and continued to break up into oidia. At the margins of the plate, where the agar ended, the mycelium grew up off the agar and formed a white filamentous growth in contrast to the mycelium in contact with the agar which habitually broke up into oidia. The filamentous mycelial growth running up the side of the petri dish later became yellowish or tawny and began to form a brownish pitted hymenium. The beginning of a hymenial formation occurred seven weeks after the oidia-forming mycelium had been inoculated on the agar plate. Three weeks later the hymenium became labyrinthiform. Since the culture was beginning to dry out seriously, the fruiting portion was transferred to a fresh plate and its growth continued. The mycelium which developed out over the surface of the plate broke up into oidia while the hymenium exhibited a tendency to become hydnoid (Plate XVIII, Fig. 2), eventually appearing the same as the previously described ones formed in the flask culture of blocks of wood and, like these, also shed copious quantities of basidiospores. A number of such transfers,

made from old oidia-forming mycelium, repeatedly resulted in the formation of a basidosporic hymenium similar to the one just described, thus completing the life history of this fungus.

Reactions of the Sporophores to External Stimuli.

Relation to Water.— Buller (1909) has ably emphasized the xerophytism of the hymenomycetous stick or log flora. While the same author has demonstrated that the sporophores of many of the wood-inhabiting fungi are able to withstand dessication unharmed — some upwards of four years — the resistance of the mycelium to dry conditions still requires experimental investigation. It may be that the xerophytism of a fungus is only partial — that dessication is fatal to the mycelium but harmless to the sporophores. However, the rapidity with which sporophores, on the event of rain, develop upon sticks which have been dessicated for weeks in the summer, points to the conclusion that the mycelium in the wood frequently must retain its vitality in a state of dessication for long periods. Bayliss (1908) was able to develop new sporophores on a stick bearing a number of sporophores of *Polyporus* (*Polystictus*) *versicolor* (L.) Fr. that had been kept four years as a museum specimen, by keeping it in a moist chamber for a month. The old sporophores, however, upon being revived, did not shed any spores but became discolored and appeared to have lost their vitality. This observation seems to prove conclusively that the mycelium in the wood must have retained its vitality for four years in the dessicated condition.

An experiment similar to the above one was tried with *Polyporus pargamenus*. A bolt of a trunk of a white oak (*Quercus alba* Linn.) was cut by the writer in November, 1914, and stored on a shelf in the cellar. In November, 1916, a section was sawn off this bolt, moistened, and kept in a moist chamber for over two months. At no time, however, could active mycelium be observed — at least none other than that of various moulds. While the writer had no

other material with which to test the vitality of dessicated mycelium, the failure of this test does not deter him from thinking that the mycelium of *Polyporus pargamenus* should retain its vitality as long as that of its near relative, *Polyporus versicolor.*

The extreme xerophytism of *Polyporus pargamenus* is shown by the ability of its sporophores to revive occasionally the second year. In the fall of 1915 the writer located a dead black oak bearing numerous sporophores of *Polyporus pargamenus* at its base. When observed, the sporophores appeared to be somewhat old and weathered, although certain of them shed copious quantities of spores upon being revived, while others shed few or none. From this fact it would appear that this crop of sporophores probably developed in the early spring of 1915. Frequent observations were made on this particular tree to determine whether a new crop of sporophores would be produced and whether any of the old ones would revive and continue growth. No growth whatsoever was to be seen until the middle of June, 1916, when it was noted that a whitish mould-like growth was appearing at the base of certain of the sporophores. On some the growth appeared on the upper surface; on others the new growth made its appearance as a new hymenium beginning to form over the old one; and in still others a new growth appeared simultaneously on both sides. Opportunity to examine the progress of this growth was not afforded until early in the fall of 1916. At this time the growth evidently was complete. The upper surfaces of certain sporophores were found to be covered with a new mold-like growth of hyphæ, causing them to appear grayish. The presence of this new layer of hyphæ gave the sporophores the appearance of being of the current year's growth. On many sporophores a new hymenial layer developed over the old one, either partially or entirely covering it. Where new growth was put out on both sides of the pilei the resulting sporophores appeared to be just as normal in structure as the original ones, excepting that they were extraordinarily thick. A few sporophores, in addition to putting out a new growth

over both the upper and hymenial surfaces of the sporophores, also enlarged extensively by outgrowths from the margins. (Plate XIX.) The revival of the sporophores of *Polyporus pargamenus* is to be attributed to a direct outgrowth from the old tissues, beginning at the base of the individual sporophore and spreading gradually to their margins. Later in the fall of 1916 the tree bearing these sporophores was cut down and burned incident to the improvement of the grounds on which it stood, so that the possibility of future observations was necessarily precluded. From the observations recorded above, however, it is evident that sporophores of *Polyporus pargamenus* which have remained in a dessicated state for nearly a year (possibly more), under certain conditions, may revive and produce a new growth in the form of surface additions, formation of a new hymenial layer and spores, or additions to the margin. Peck (1880) has likewise observed that this plant sometimes revives to a certain extent the second season by putting on a new hymenium and a new growth from the margin of the pileus. In addition the writer has also observed the revival and growth of old sporophores taking place frequently when blocks from logs bearing sporophores are kept in a moist chamber for a few weeks.

Buller (1909, p. 111), in a list of Hymenomycetes with sporophores which can become dessicated without losing their vitality, states that the sporophores of *Polyporus pargamenus* recovered after dessication for one year, the recovery being judged by their ability to shed viable spores upon being revived. The xerophytism of the plant is further exemplified by the ability of the spores to germinate and produce infectious mycelium, after having been shed and kept in a state of total dessication for ten months, as described earlier.

Gravity and light both play a very important role in determining the development and direction of growth of the sporophores of many of the Agaricales, so that it is not surprising to find that the combined action of these two stimuli is necessary for the development of a perfectly formed sporophore.

Relation to Gravity.— Under natural conditions the pileus is invariably horizontal while the hymenial tubes are vertical. It can be proved by simple experiment or by observations of instances of natural occurrence in the woods, that the pileus is diageotropic and that the tubes are positively geotropic. Trunks of trees that are covered with young pilei of *Polyporus pargamenus*, and then subsequently break off, are commonly met with in the woods. Quite frequently the trunks fall so that the margins of the pilei project vertically upward or at least come to lie in a more or less perpendicular direction. Under these conditions all new growth from the margins of the pilei develops in such a manner that the upper surfaces of the subsequently formed portions of the pilei are brought into a horizontal plane. When this has taken place the pilei become diageotropic and now expand rapidly in a direction parallel to the earth's surface. At the same time hymenial tubes develop from the lower surface of the newly formed portions of the pilei. They are positively geotropic and grow vertically downward. The original pilei, now in a vertical position, soon cease to grow and all new growth is concentrated in the new, horizontally forming portion of the pilei. It thus becomes evident that the stimulus of gravity strongly favors the growth of the horizontally placed portions of the pileus. In all cases the hymenial tubes develop and grow vertically downward, thus reacting in a positively geotropic manner. It has been noticed repeatedly in a number of different species of polypores that newly formed sporophores, whose positions have become reversed through the overturn of the wood upon which they were growing, always would tend to restore themselves to their original and normal position in their subsequent growth. Spaulding (1911, p. 17) gives an account of an instance of this in the case of *Lenzites sæpiaria* (Wulf.) Fries. A railroad tie, with a newly formed sporophore upon it, had been turned with its former surface underneath, so that the gills were on the upper instead of the under surface of the sporophore. When found the gills had just begun to produce a new growth of mycelium. On the sixth day new gills began to form on the

former upper surface of the fruit-body and on the eighth day the transformation was complete. The writer has found sporophores of *P. pargamenus* which had had their hymenial surfaces turned uppermost owing to a reversal of the substratum. When found the pilei already had enlarged from one-fourth to one-half inch in breadth since becoming inverted, the new growth being reversed with respect to the position of the old. In other words the original hymenial surface abruptly changed to the upper surface of the new portion of the sporophore while the original surface became overgrown with a hymenial layer. The time required for such a change, however, would be but little or no greater than that required for normal growth and would vary with the climatic conditions.

It appears then that the stimulus afforded by gravity decides not only the direction of the growth of the pileus and hymenial tubes, but also which part of the sporophore shall develop and where the tubes are to be formed. In other words, gravity acts upon the fruit-body both as an orienting and as a morphogenic stimulus. As Buller (1909) has so ably pointed out in his "Researches on Fungi," the geotropic reactions enable the hymenial tubes to be developed in such a position that, with a given diameter, the maximum number of them may be produced in such a position as to be quite protected from rain and that the spores may fall out in the easiest possible manner.

Relation to Light.—A portion of a fallen trunk (three inches in diameter) of the wild red cherry (*Prunus pennsylvanica* Linn. f.) with numerous sporophores of *Polyporus pargamenus* beginning to make their appearance on it, was brought into the laboratory. Two pieces about four and one-half inches long were cut from this stem, immersed in water for a time, and placed into two glass culture jars. These blocks of wood were placed in the jars in the same positions with respect to gravity that they occupied in the field. Both jars were placed side by side on a table in the laboratory, one being covered with a light-proof pasteboard box, and the other, kept exposed to the light of the laboratory, was used

as a control. At the beginning both blocks of wood bore partially formed sporophores on the sides and under surfaces, but on the tops the mycelium was just appearing through the lenticels and had not begun to differentiate into the parts of a sporophore. In a few days a floccose growth appeared from each of the lenticels of the block kept in darkness. Soon after this these hyphal growths assumed the form of loosely interwoven bosses. In the case of the block kept in the light a slow scant growth was made by the mycelium but it was of a compact leathery nature and never loose and fluffy as was the growth made in the dark. In addition the mycelium which developed in darkness made a much greater and more rapid growth than that which developed in the light of the laboratory. It was evident that the absence of light stimulates the mycelium to a much greater vegetative growth than otherwise would occur. After a month the mycelium put forth from each lenticel, which at first appeared as a fluffy boss, became more or less compacted and spongy in consistency. In no case, however, did any sporophores form on the block kept in the dark. Even the embryonic ones originally present failed to develop farther and became covered over by the outgrowth of mycelium. On the block kept exposed to the light of the laboratory, however, the mycelium developed into a number of imbricate sporophores which shed copious quantities of spores.

This experiment points to light as the controlling factor in sporophore production, although no account has been taken of the combined action of light and gravity. Experiments were made on a similar form with this idea in view by Bayliss (1908) as follows: Two small branches bearing normal sporophores of *Polyporus* (*Polystictus*) *versicolor* were secured. One branch was attached horizontally to a clock clinostat and the other used as a control. The apparatus was set up outside of the laboratory window where the branches had the advantages of ordinary atmospheric conditions and could be assured of a continuous supply of moisture by means of a dripping device. Never, however, during the several months' duration of the experiment did a typical

dimidiate sporophore form. Only small, white waxy bosses appeared and these spread irregularly in all directions, sometimes uniting with one another; later they formed an incrustation over the surface of the branch. The white waxy bosses soon turned cream color and showed signs of pore formation on the exposed surface, while the surface next to the bark assumed the velvety zoned appearance so characteristic of the upper surface of a normal pileus. A piece of the pore-forming part, laid on a glass slide for an hour, yielded a good supply of spores. On the control a well-developed series of imbricate sporophores appeared.

From these experiments it seems quite evident that the dimidiate form of the sporophore is not to be ascribed, either solely to the stimulus of light nor yet to that of gravity, but to the combined action of both. It is very evident, however, that the formation of pores, and thus spore production, is a response to the one tropism only — that of light. We see that light likewise acts upon the sporophore as a morphogenic stimulus, and much more strongly than the tropism induced by gravity.

Relation to Chemotropism.— Studies were made upon germinating spores and pure cultures of *Polyporus pargamenus* in order to determine whether the mycelium would respond to chemotropic stimuli. Spores were germinated in hanging drops of nutrient medium in which thin sections of yellow birch wood had been placed. The germ tubes, however, continued to grow according to their own inclinations and the direction of growth did not seem to be influenced by the presence of a section of wood in the hanging drop. Bayliss (1908) observed the same behavior for *Polyporus* (*Polystictus*) *versicolor.*

Transfers were made from pure cultures of *Polyporus pargamenus* to plates containing a rich malt agar, on top of which (in the center of each plate) a small, sterile block ($\frac{1}{4}'' \times \frac{1}{4}'' \times 1''$) of yellow birch wood had been placed. The inoculations were made on the agar beside the blocks of wood, the whole experiment being performed under sterile conditions. In a few days the mycelium completely envel-

oped the blocks in a luxuriant growth and eventually filled the whole dish. At the end of two months the blocks were examined and exhibited but little or no evidence of decay. The results would indicate that the mycelium of this fungus, at least so long as food is readily available, will take it from the source of least resistance — in other words, the source from which the food can be most easily assimilated.

Regeneration of Lost Parts of Sporophores.—As is commonly the case in the less highly organized plants, the lost parts of their structures often are replaced — a direct regeneration thus taking place. This procedure is of especially common occurrence among the sporophores of the wood-destroying fungi but the regeneration is limited to actively growing sporophores. The regeneration of lost parts can be demonstrated readily in *Polyporus pargamenus* by cutting off carefully a portion of the pileus or even the hymenium alone. It is only a matter of a few days, in case conditions for favorable growth are present, for the lost part to be entirely restored.

The Destruction of Wood by Polyporus Pargamenus.

Chemistry and Physics of the Decay.

Wood decay in general consists of a series of chemical and physical changes brought about by the action of the mycelium of the fungus. As in other wood-destroying fungi, the decay caused by *Polyporus pargamenus* is essentially a process of digestion and absorption. The digestion of woody tissues by this fungus is due to the excretion of a number of enzymes or organized ferments which reduce the woody substance to simpler organic compounds capable of being absorbed through the walls of the mycelial filaments, and which determine the manner of the decay of the woody substance. It is by means of their enzyme excretions that the minute and delicate, thin-walled fungal hyphæ are enabled to dissolve their way through the lignified membranes of their host. This action is comparable to that of the ferment secreted by yeast cells in breaking down sugar. After the fungal hyphæ

of *Polyporus pargamenus* have penetrated the lignified membranes of their host in all directions they continue to exert on the cell-walls a solvent action which extends over a considerable area. In this way the original holes dissolved through the cell-wall continue to enlarge. When the enzyme excretions have accumulated to a sufficient amount the dissolution of the cell-walls becomes wide-spread and entire lamellæ disappear in a definite sequence.

The dissolution of the cell-walls is to be attributed to the fact that they, as a potential source of food, are valueless to the fungus until broken down and reduced to a condition suitable for translocation and assimilation. The transfer of the food materials through unbroken cell-walls to the various points of consumption can be accomplished only when they are in solution. In other words, they must first be converted into soluble substances capable of osmosis in order to be utilized by the fungal hyphæ. The agents instrumental in bringing about these changes belong to those substances termed ferments or enzymes — substances which possess the power of decomposing or transforming certain organic compounds into other substances without themselves being changed or consumed in the process. By virtue of this property they are enabled to transform unlimited quantities of certain substances if the resulting product be continuously removed, as would be done by the fungal hyphæ developing and ramifying through the woody substance. The peculiar manner in which enzymes act is illustrated by the following examples.

In the diastatic transformation and dissolution of starch the starch grain is not dissolved from the surface inwards as a homogeneous crystal, but becomes corroded by narrow canals until finally it is completely disorganized and disintegrated. The reduction of woody tissues by fungal hyphæ offers another example. Wood is generally considered to be made up of a complex lignocellulose, comprising such higher carbohydrates as lignin, cellulose, hemicellulose, and pectic bodies. Each of these respective carbohydrates may be split into simpler constituents by being acted upon by the accom-

panying cyto-hydrolytic enzyme. For instance, ligninase, called hadromase by Czapek (1899), designates the enzyme capable of splitting lignin; cellulase, the true cellulose-hydrolyzing ferment; hemicellulase, the ferment hydrolyzing hemi-cellulose; and pectinase, an enzyme which hydrolyzes into reducing sugars the pectinous substances, especially the middle lamellæ of plants. All of these different enzymes and many others, when present, enact a definite role in the dissolution of the woody substance.

Recent investigations prove conclusively that, in order to accomplish the dissolution of the woody substance, each wood-destroying fungus secretes a number of different enzymes, each of which is so specialized that it acts only on certain individual substances or groups of related substances. Furthermore, these various enzymes may act simultaneously. In a word, enzyme action is the strategic center of vital activity. The chemical action induced by such agents causes a rapid dissolution of certain constituents of the cell-contents and the cell-walls of the wood, the ultimate product being a reduced, disintegrating mass which crumbles readily under the slightest pressure.

In all cases, regardless of how the decay proceeds or what constituents are removed from the wood, there is a momentous change in its physical character. This change is most strongly exemplified by the decrease in its specific gravity. In case the fungus has delignified the cell-walls of the wood, partial or complete collapse occurs, since it was through lignification of the fundamental cellulose wall originally that the essential element of strength was afforded.

The ultimate effect of *Polyporus pargamenus* is to reduce the essential physical properties of the wood attacked and thereby lessen or completely destroy the utility and consequently the value of the timber.

The Decay of Yellow Birch Wood.

Structure of Normal Wood. — Macroscopically the wood of yellow birch (*Betula lutea* Michx. f.) is heavy, hard, and strong, but not durable when exposed. The sapwood is a

light yellowish brown color, the heartwood somewhat darker, there being no sharp line of demarcation between them. In a transverse section of the wood the pores are numerous, indistinct to the unaided eye, and uniformly distributed throughout the growth ring. The pith rays likewise are mostly indistinct without a lens.

Microscopically the wood of yellow birch presents the usual features of the diffuse-porous type. The annual rings are defined principally by a tangential row of wood parenchyma which terminates the growth ring. The definition of the annual rings is somewhat further enhanced in that the vessels are slightly smaller and more sparsely distributed in the late wood. (Plate XXI, Fig. 1.) Microscopically the wood of the yellow birch is seen to consist of (a) uniseriate and multiseriate pith rays, (b) pitted vessels, (c) metatracheal parenchyma with simple pits, and (d) wood prosenchyma with either simple or bordered pits. The medullary rays are from 1–3, more rarely 4, seriate, and homogeneous. The ray cells are mostly elongated in a radial direction and are connected with one another by numerous simple pits. As units the rays are peculiar in that the lateral walls of the uniseriate forms and similarly the lateral walls of the peripheral cells, in the case of the multiseriate forms, are characterized by having very thin walls, while the interior cells in the latter case have fairly thick walls. The vessels occur either solitary or in radial groups of from two to three; they are uniform in size and distribution throughout the growth ring. Their walls are comparatively thin and densely covered with small bordered pits with narrow, slit like openings. These occur on the contiguous walls of the vessels and where they are in contact with wood or ray parenchyma. The vessel segments are characterized by very oblique end walls which are provided with numerous scalariform perforations. A small amount of wood parenchyma is scattered irregularly throughout the growth ring (metatracheal), sometimes appearing in broken tangential lines in the late wood.

The individual cells of wood parenchyma are characterized by very thin walls (much thinner than those of the wood prosenchyma elements) and abundant simple pits, particularly on their end walls. On the other hand the wood prosenchyma of yellow birch offers the usual features. It is characterized, however, by elements provided either with small simple pits, or more rarely, small but distinctly bordered pits. (Fig. 5.) In shape and size the bordered pitted elements resemble wood fibers rather than tracheids.[16]

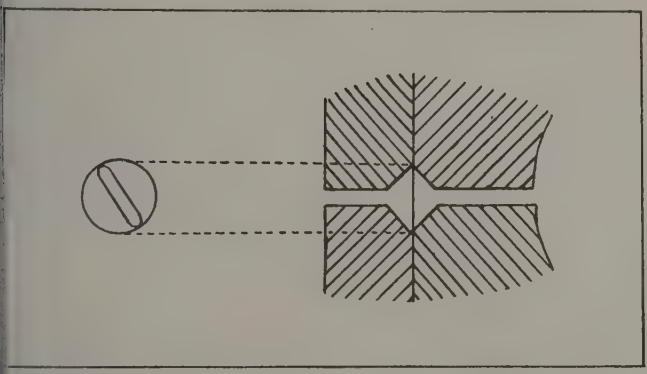

FIG. 5.
Bordered pit in yellow birch (*Betula lutea*) wood, transverse section, X, 3,000.

Microchemical Reactions of Normal Wood.— The course of the destruction of the cell walls and the chemical changes occurring in them can be observed readily by studying temporary mounts of sections of decayed wood treated with the various microchemical reagents commonly employed for the recognition of cellulose and lignin. Studies of this kind,

[16] Many authors avoid distinguishing between such similar elements as wood fibers and tracheids by classifying both as wood prosenchyma. In many woods all gradations occur in the pitting of these elements from simple pits on the one hand to semi-bordered or bordered pits on the other hand.

however, should be preceded by a study of sections of normal wood treated with these respective reagents in order to determine the relative degree of lignification of the various woody elements and any structural peculiarities that would aid materially in explaining the course of the decay in the wood.

Normal wood, when treated with chlorzinc-iodine, shows the presence of considerable cellulose. The middle lamellæ of all the cell-walls become colored golden brown. The wood prosenchyma elements are peculiar in that the tertiary layers (layers bordering on the cell lumina) assume a pronounced violet coloration which extends into the secondary layer but is only faintly perceptible in the primary layer or middle lamella. The violet coloration assumed by the tertiary layer of the wood prosenchyma cells, however, diminishes in intensity toward the outer margin of the growth ring until it is scarcely discernible in the elements of the summerwood. The vessels, pith-ray cells, and thin-walled wood parenchyma fibers exhibit only a golden brown coloration with chlorzinc-iodine. Tests for lignification were made with phloroglucin-HCl, aniline sulphate-H_2SO_4, resorcin-HCl, phenol-HCl, orcin-HCl, and thymol-HCl, each reagent exhibiting its respective color reaction throughout.

In sections of wood treated with phloroglucin-HCl the vessel walls and middle lamellæ of all the cells are stained most strongly, becoming old rose or wine-colored. The coloration assumed by the middle lamellæ is especially pronounced in the terminal cells of the growth ring. The remaining layers of the medullary ray and wood parenchyma cells also become rose-colored. The secondary and tertiary layers of the prosenchyma elements are colored almost uniformly rosy-violet — at least they are considerably lighter than their middle lamellæ. When sections are treated with aniline sulphate-H_2SO_4 the vessel walls and the middle lamellæ of all the cells stain most deeply, becoming golden yellow. The remaining layers of the medullary ray and wood parenchyma cells stain only to a pale lemon color. The secondary and tertiary layers of the prosenchyma elements remain quite pale in contrast to their middle lamellæ, they

take on merely a yellowish tint, excepting in the terminal cells of the growth ring where they become somewhat more strongly colored.

From the tests described above in full detail, and from still other tests employed for the differentiation of both cellulose and lignin, it is evident that the entire vessel walls and the middle lamellæ of the other elements are lignified to a much greater degree than the secondary and tertiary layers of these elements and that the tertiary and secondary layers of the wood prosenchyma elements are lignified to an approximately equal extent. As a result of the variable structure and microchemical reactions of the various elements, we naturally would expect to find that the vessel walls would resist delignification longer than any one part of the other cells. Of the latter the middle lamellæ would be far more resistant to the solvent action of the fungus than the secondary and tertiary layers of these respective elements. In the description of the course of the decay, which is given later, we shall see to just what extent this inference is substantiated.

Macroscopic Appearance of Decayed Wood.—The first evidence of incipient decay in yellow birch wood is the appearance in the wood of small, irregular areas in which the tissues have lost their natural brownish color and appear as though bleached. The wood between the lighter areas remains moderately sound for a time, at least it does not begin to decay until they are considerably disintegrated; even then their decay proceeds very slowly. All parts of the annual ring are equally susceptible to the attacks of the fungus.

Cross sections of trunks in the early stages of decay usually exhibit a number of conspicuous, irregular zones of blackish wood which sharply delimit decayed from sound wood or portions of the wood in different stages of decay. In cross sections of partially decayed trunks these black zones in the wood have the appearance of irregular lines. Longitudinal sections show that they extend for varying distances up and down the stem, their general course being parallel to the

elements of growth. They are not limited by the annual rings, however, for they may cross and recross these repeatedly. Examination shows that these black zones consist of wood of unusual hardness. As shown in a previous paper by the writer (1917[2]), these black zones are caused by the infiltration into the wood of decomposition products formed from the woody substance as it decays. They are of common occurrence in the decay of all dicotyledonous woods by *Polyporus pargamenus* and other wood-destroying fungi, but appear to be of comparatively rare occurrence in the decay of coniferous woods. Further discussion of black zones will be presented later.

Yellow birch wood in an advanced stage of decay has a mottled appearance. The decay is localized mainly in minute areas, each of which is bounded by a thin zone of firmer wood. The areas of advanced decay appear as white spots while the less decayed wood bounding these is more or less yellowish and resembles superficially a delicate network (Plate XX) visible on all three sections. This network is rather inconspicuous in dry wood but stands out quite prominently after the surface of the wood has been moistened.

As the solvent action of the fungus progresses, the white, decayed areas, or pockets, continue to enlarge. Within the individual centers of decay the disintegration progresses in a direction parallel to that of the woody elements and in time the woody elements in these respective areas are reduced rapidly both in color and hardness until they become pith-like.

This method of decomposition results in the formation of a series of pronounced pockets or cavities within the wood (Plate XXI, Fig 2). In the latter stages of the decomposition two or more decayed areas frequently coalesce into one so that the wood has a decided "pocketed" appearance. Although highly irregular in size and outline, the largest of these decayed areas, or pockets, as bounded by the meshes of firmer yellowish wood, average two mm. or less in diameter and one cm. or less in length. In general their length coincides with the direction of the woody elements, although

occasionally they may extend at right angles to them. At this stage they are quite empty of contents save for a few scattered tubular elements — the vessels. Owing to their greater lignification, these elements are the last to disappear under the dissolving action of the fungus. In time, however, even these disappear, leaving practically nothing within the pockets, which by this time are separated by almost membranous layers of woody tissue merely a few cells thick. (Plate XXIV, Fig. 1.) Numerous strands of white mycelium, running both longitudinally and radially through the decayed wood, can be seen with the unaided eye. By the time the decay has progressed to this point, the wood has lost all of its original characteristics of color, odor, hardness, and strength, and has become a bleached mass of pithy consistency.

Blocks of wood cut from a decayed log and kept in culture chambers decayed much more rapidly than they normally would under field conditions. In a few weeks they became covered with a growth of mycelium which thrived for several weeks. After that time the growth of the mycelium seemed to cease and portions of the mycelial mass died and became discolored. Portions of these blocks of decayed wood were even softer in texture than a wet sponge and the decay seemed to have progressed to its utmost extent since the mycelium within the woody tissue apparently was functioning no longer. The decayed wood appeared like a honeycomb composed of the finest and most delicate, whitish membranes. By this time the decayed pockets had fused together to such an extent that some were found to measure three mm. in diameter and to extend lengthwise through the wood for three cm. It may be assumed with reasonable certainty that the wood at this time was in the final stage of decomposition for we have no reason to think that woody tissue must be entirely destroyed in order that the specific decay be completed. It is only natural to suppose that the growth of the mycelium will terminate when the nutrient substances have been extracted reasonably thoroughly from the woody tissue. It is definitely known that wood-destroying fungi, owing to

their power of disorganizing their own substratum by fermentation and putrifaction, not only cause the substratum to become an unfavorable nutrient medium for the entrance and growth of other fungi but may in time render it unfit for their continued growth. Under normal conditions the woody tissue that has been reduced partially by cellulose and lignin ferments will of course be attacked by molds, bacteria, and other micro-organisms and split up into simpler compounds. It is to these agencies that we must attribute the final reduction to "humus" of the refuse material left from woody tissue after its partial destruction by the more potent agencies — the wood-destroying fungi.

The outer, paper-like bark of the yellow birch is exceptionally resistant to decay. Yellow birch trees frequently are found with this outer bark sound and entire while the inner portion of the bark and all of the underlying wood may be completely rotted, either by this or by other wood-destroying fungi. This great resistance to decay, according to Stevens (1910, p. 336), is to be attributed to the presence of betulin — a glucoside which occurs in the form of fine granules in thinner-walled cork cells of birch bark. This is strongly antiseptic and protects birch bark against the attacks of lower organisms.[17] The inner, brown fibrous bark, however, is speedily decayed by the action of the fungus and is converted into a whitish crumbling mass, which can be pulverized readily between the fingers to a gritty powder containing a large percentage of a crystalline substance, doubtlessly calcium oxalate.

Microscopic Characters of Decayed Wood.— In sections of wood in an advanced stage of decay, all stages of decomposition, from incipient delignification to the complete disappearance of the elements, may be seen. Separating the pockets or decayed areas are irregular zones of less decayed wood (Plate XXI, Fig. 2) varying from a few to several cells wide. In the median cells of such zones, all three layers

[17] Outer bark of any kind, however, would be quite resistant to decay, owing to its corky nature.

of the cell-wall of the prosenchyma elements respond to lignin tests as they do in normal wood. The cells bordering on these elements are in various stages of decomposition. In some the tertiary layer no longer gives the characteristic color reactions when treated with various lignin reagents, but remains colorless. In other cells the secondary lamella of the cell-wall also remains colorless and undoubtedly consists of practically pure cellulose. As a general rule, both the secondary and tertiary layers remain in place until after all of the cell-wall but the middle lamella is delignified, whereupon the destruction of the cellulose commences. Those layers of the cell-walls that remained colorless after treatment with lignin reagents take on a pronounced violet color when treated with cellulose reagents such as chlorzinc-iodine. Groups of these cells sometimes are seen in which the middle lamellæ are colored brown with chlorzinc-iodine, while the secondary and tertiary layers are colored a deep violet and frequently exhibit a pronounced swelling. If sections are subjected to the action of chlorzinc-iodine for several hours, the cellulose layers swell up to such an extent that the cell lumina often entirely disappears. The behavior of these membranes with chlorzinc-iodine affords a double proof of their cellulosic nature; first, by reason of the violet color assumed, and second, by reason of the swelling of the cell-membrane after the application of this reagent.[18]

It is evident from the above description that the dissolution of the cellulose does not occur within any one cell until some time after its wall, the middle lamella excepted, has become completely delignified. Within the individual cell, the cell corners, where the middle lamellæ often are thickened characteristically, respond the longest to tests for lignin. Owing either to the fundamentally different composition of the basic principle of the middle lamella or to its subsequent infiltration by lignin constituents, it resists decay longer than

[18] This swelling of decaying membranes is too often attributed to the action of the fungus effecting the decay. As a general rule, the swelling does not occur until after the application of chlorzinc-iodine, and the swelling is to be attributed to the action on the cellulose of the excess zinc chloride found in this reagent.

the secondary layers and remains in place long after the disappearance of the secondary and tertiary lamellæ of the cell-wall. After the secondary layers of thickening have been dissolved, the resulting woody tissue has a skeletonized appearance (Plates XXII and XXIV, Fig. 1). It has all of the elements but their walls consist principally of the middle lamellæ. These retain the nature of lignified walls and offer considerable resistance to dissolution, and are the last portion of the individual cell-wall to disappear. However, they too gradually become thinner and thinner until they break up into irregular fragments. It is not until they have disintegrated to this extent that the middle lamellæ respond to the cellulose test with chlorzinc-iodine. The corners of the middle lamellæ, where they are thickest, are the last to disappear.

Within the decayed areas the uniseriate pith-rays frequently are dissolved out quickly early in the course of the decay. These are the first elements to disappear and doubtlessly disappear first because of their exceedingly thin cell-walls, as explained earlier. Frequently the medullary rays are dissolved entirely while cell-walls of normal thickness may be found immediately adjoining them on both sides (Plate XXII). The thick vessel walls are strongly lignified and are the last elements to disappear. They continue to respond to tests for lignification long after the surrounding cell-walls fail to do so and frequently persist quite intact while the surrounding cell-walls are dissolved until only the middle lamellæ remain. In still later stages of decay, the partially disintegrated vessel walls often are the only elements remaining within the pockets. They are retained in their original positions within the pockets by reason of being held in place by numerous mycelial threads which penetrate their walls in all directions. Where two or more vessels are contiguous, they frequently separate before they are entirely dissolved. Where they remain attached until completely decayed, however, the common walls between two or more vessels are the last portions to be decomposed by the action of the fungus. Finally even the resistant vessel walls become

so much eroded that they break up into irregular fragments, among which can be detected portions of pitted walls and scalariform bars from the end walls of the vessel segments. Even those fragments of vessel walls retain their lignified nature until they become almost completely dissolved. Within any one center of decay the dissolution of the cell-walls progresses very uniformly, as shown by the fact that the distance from normal cell-walls to walls that have been completely decayed is often no more than thirty-five microns.

An examination was made of prepared slides for the purpose of determining the relation of the mycelium to the wood. In the earlier stages of the decay the hyphæ may follow the course of the vessels and wood parenchyma elements for some distance before diverging, and again they may branch off profusely and enter the medullary rays. In the much decayed wood the mycelium is abundant in all the woody elements and branches profusely in all directions, perforating the walls of the woody elements at random. In the later stages of the decay it is evident that many of the hyphæ deliquesce, or, at least, disappear in some way, for the perforated cell-walls are commonly seen but no hyphæ can be found associated with them. The hyphæ found in decaying yellow birch wood are exceedingly delicate and minute. No cross-walls or clamp connections were observed in them although failure to see these structures may have been due to the extremely small size of the hyphæ. Dense plugs or mats of hyphæ frequently occlude the vessels. These mats of hyphæ are brown by reason of being incrusted with some decomposition product.

From the above study it is evident that the first main chemical change which is brought about by the action of the fungus is that of delignification. It is due to this action that the elements lose their normal brownish color and appear as though bleached. At the beginning of delignification, the decay seems to be localized in small areas which appear as pockets in the wood after the woody tissue within them is completely destroyed. From the results obtained, it is apparent that delignification commences in the tertiary layer

and proceeds toward the middle lamella. After the cell-wall is delignified down to the middle lamella, the reduction of the cellulose commences. With the destruction of the cellulose, nothing is left but a skeletonized framework of middle lamellæ, which in turn break up and undergo complete reduction. Within a pocket or unit area of decay, all stages of decomposition from incipient to final may be seen within the range of a few cells (Plate XXI, Fig. 2).

The Decay of Sugar Maple Wood.

Structure of Normal Wood.— The wood of the sugar maple (*Acer saccharum* Marsh.) is heavy, hard, strong, and close-grained, but is not durable in the soil or otherwise exposed. The sapwood is creamy white while the heartwood is light brown tinged with red, there being no sharp demarcation between them. In a transverse section of the wood, the pores are numerous, indistinct to the unaided eye, and uniformly distributed throughout the growth ring. The pith-rays, while not conspicuously broad, are very distinct without a lens.

Microscopically the wood of sugar maple presents the usual features of the diffuse-porous type. The growth rings are distinct and regular in outline; their width, however, is subject to considerable variation. The wood is seen to consist of (a) uniseriate and multiseriate pith-rays, (b) pitted vessels with spiral thickenings, (c) scanty wood parenchyma which is mostly paratracheal, and (d) wood prosenchyma with simple pits. The pith-rays are composed of small, homogeneous, radially elongated cells bearing numerous simple pits. Part of the rays are comparatively large — from five to seven cells wide — and many cells high. The intermediate rays are mostly uniseriate. The vessels are distributed uniformly throughout the growth ring and diminish gradually in size from the spring to the summerwood. The vessel segments, which do not possess large lumina, are comparatively thin-walled, provided with simple perforations at the ends, and are characterized by spiral thickenings. The

vessels occur singly or in radial groups of from two to five, or rarely six. The vessel walls, at their points of contact with one another and where they border on ray or wood parenchyma, are provided with densely packed and rather large bordered pits, the borders often hexagonal owing to crowding. The interior walls of the vessels are provided with spiral thickenings. The wood parenchyma is developed to a limited extent, the walls remaining comparatively thin. It occurs sparingly on the radial sides of the vessels and is also to be found scattered irregularly over the outer face of the summerwood. The individual cells of wood parenchyma, as well as the ray parenchyma, responded to the iodine test for starch, since the wood was cut late in the autumn. Chambered parenchyma containing crystals occurs occasionally but was by no means common in the sapwood studied. The wood prosenchyma has simple pits and the elements are of the nature of typical wood fibers. These elements sometimes contain starch. The growth rings are defined mainly by a tangential flattening of the outermost cells and by the somewhat smaller size of the vessels in the late wood (Plate XXIII, Fig. 1).

Microchemical Reactions of Normal Wood.— Cross sections of normal wood, when treated with cellulose reagents such as chlorzinc-iodine, exhibit comparatively little of the characteristic violet coloration indicative of cellulose. The middle lamellæ of all the cells and the entire walls of the vessels and medullary rays all color yellowish-brown. Certain of the prosenchyma elements, particularly those on the outer face of the late wood, exhibit a slight violaceous coloration in the secondary and tertiary layers. The majority of the prosenchyma elements, however, exhibit little or no such coloration with chlorzinc-iodine. In sections of wood treated with phloroglucin-HCl the vessel walls and the middle lamellæ are colored most strongly, becoming reddish-violet. The remaining layers of the medullary ray cells likewise become reddish-violet and appear to be stained almost as deeply as the vessel walls. The secondary and tertiary

layers of the wood prosenchyma elements are colored much less strongly than their middle lamellæ and appear to be almost violaceous or violaceous tinged with red, especially in the terminal cells of the growth ring. When sections are treated with aniline sulphate-H_2SO_4, the vessel walls and the middle lamellæ of all the cells stain golden yellow. The remaining layers of the medullary ray cells appear brownish-yellow. The secondary and tertiary layers of the wood prosenchyma elements stain much lighter than their middle lamellæ, becoming a pale lemon color.

From the tests described above in full detail, and from still other tests employed for the differentiation of both cellulose and lignin, it is evident that the vessel walls are lignified to a much greater extent than any other one element excepting the multiseriate pith-rays. Of the individual cells, the middle lamellæ are lignified far more strongly than the secondary layers. The secondary layers of the wood prosenchyma elements, therefore, are the least strongly lignified tissues of the wood. The lignification of these elements, however, increases markedly on the outer face of the growth ring. As a result of the dissimilar structure and the microchemical reactions of the various elements, we naturally would expect to find that the vessel walls and the broad medullary rays would resist decay longer than any other element. Of the other elements the middle lamellæ would be more resistant to the solvent action of the fungus than the secondary layers of thickening possessed by these respective elements. We also would expect to find that the terminal margin of the growth ring would resist decay longer than the remainder of the growth ring. When it is understood that the first result of the decay caused by this fungus is the delignification of the woody substance, it would be expected that those elements which are strongly lignified (the vessels, medullary rays, and the terminal cells of the growth ring) will resist destruction far longer than the less lignified elements (the wood prosenchyma).

Macroscopic Appearance of Decayed Wood. — The decay of sugar maple wood is very similar to that of yellow birch,

which has been described in full detail so that it may serve as a type. The decay of sugar maple differs from that of yellow birch only in the following respects. The pockets, which are highly irregular in outline, are much broader as viewed radially than in the tangential section. On the radial surface of the decayed wood examined, the largest pockets were one cm. long and five mm. wide; on the tangential surface, however, the largest pockets were not over two mm. wide. The tendency for the pockets or decayed areas to enlarge mostly in a radial direction is explained by the peculiar structure of the wood. The wood is of homogeneous structure except for the numerous broad pith-rays which transverse the growth rings in a radial direction. Examination of a transverse section of decayed wood reveals the fact that the broad medullary rays, the outer margin of the growth ring, and the vessels are the last elements of the growth ring to decay. The broad medullary rays offer exceptional resistance to the spread of the decay in other than a radial direction. The vessels remain behind until long after practically all the other elements in the growth ring between the broad medullary rays have been dissolved out. At this stage of the decay the vessels appear as isolated capillary tubes loosely held between the medullary rays by partially disintegrated tissue. The numerous broad medullary rays which transverse the annual rings of growth in a radial direction serve to bind together the layers of growth so that there is no separation of the decayed wood along the line of the annual rings. The numerous broad medullary rays act like so many reinforcing structures so that the decayed wood responds far less to tangential compression than to radial compression. They likewise materially increase the transverse breaking strength of the decayed wood. As a result of the strengthening effect afforded by the medullary rays of this wood, a trunk of sugar maple rotted by *Polyporus pargamenus* would be less subject to breakage than a similar trunk of yellow birch rotted to the same extent by the same species of fungus. The difference in the appearance of the decay by this fungus of two woods so similar in their general

structure is noteworthy when one considers that these differences are brought about solely by minor structural differences of certain elements of these respective woods, in this case the elements being the medullary rays.

The inner fibrous bark of the sugar maple decays quite rapidly and soon becomes soft and spongy. The outer scaly bark, however, owing to its corky nature, is quite resistant to decay.

Microscopic Characters of Decayed Wood.— The dissolution and course of the delignification of the woody elements is essentially the same as that described for yellow birch. In fact it differs from the decay of yellow birch only in so far as would be necessitated by the different structure of sugar maple wood.

The solvent action of the fungus proceeds very irregularly. Often cells, whose entire walls still respond strongly to lignin tests, are left among cells which have been decomposed to such an extent that only the middle lamellæ remain. The wood prosenchyma and wood parenchyma elements are the first elements to disappear. In this connection it will be remembered that these elements were less strongly lignified than any of the other elements of the growth ring. In sections of badly decayed wood, the effect of the numerous large pith-rays in retarding the decay from spreading tangentially is strongly exemplified. In addition, the terminal cells of the growth rings, which are very resistant to decay, are potent factors in retarding the spread of the decay in a radial direction. Their retarding effect, however, is less than that offered by the medullary rays. As a result of the structure of the wood and the method of decay induced by this fungus, the decay necessarily would proceed most rapidly up and down the stem, less rapidly in a radial direction, and least rapidly in a tangential direction. Within each growth ring the wood elements which adjoin the vessels decay less rapidly than the more distant-lying ones, excepting the few layers of tangentially flattened cells on the outer face of the growth ring. In sections of wood in an advanced stage of decay, aside from this resistant zone of wood, the vessels with a

few adjoining cells may be the only elements left of the original tissue of the growth ring lying between the pith-rays. (Plate XXIII, Fig. 2.)

Longitudinal sections of decayed wood showed a great abundance of matted growths of fungal hyphæ which, in addition to occluding the vessels, often extended across a great number of elements, sometimes forming veritable zones through the wood. As in the decaying yellow birch wood, these mats of hyphæ appear to be encrusted with brown decomposition products.

The fungal hyphæ apparently did not exert any solvent action on the crystals of calcium oxalate which were of occasional occurrence in the chambered wood parenchyma cells, since they remained intact despite the complete decay of the cells containing them.

Sections (taken near the black zones) of wood in the early stages of decay, exhibited considerable quantities of decomposition products infiltrating various portions of the wood. These decomposition products were most abundant in the vessels where they appeared as individual brown globules or more often a number of globules had coalesced into a brown, gummy mass completely occluding the vessels in a number of places.

These brown, gum-like masses dissolve slowly and without heating when allowed to stand in a 5 per cent solution of potassium hydroxide for a few hours.

The Decay of Bitternut Hickory Wood.

Structure of Normal Wood.— The wood of the bitternut hickory [*Hicoria minima* (Marsh.) Britton], is heavy, hard, moderately strong, and tough, but is not durable in the ground or if exposed; the sapwood especially is always subject to the inroads of boring insects and fungi. The sapwood is white and characteristically narrow; the heartwood is of a reddish nut-brown color. The pith-rays are abundant but not conspicuous. The wood parenchyma is arranged in fine tangential lines which do not appear as distinct as the rays.

Microscopically the wood of bitternut hickory presents the usual features of the ring-porous type. The growth rings are fairly well defined by the zonate arrangement of the large vessels in the early wood of the growth ring and by the tangential flattening of the cells on the outer face of the late wood. In the late wood the vessels become fewer, smaller, and scattered; the larger ones of the early wood are characterized by their abundance of tyloses. The wood of the bitternut hickory is seen to consist of (a) uniseriate and multiseriate pith-rays, (b) pitted vessels, (c) metatracheal zonate wood parenchyma, and (d) wood prosenchyma with both simple and bordered pits. The pith-rays, which are composed of small, mostly radially elongated, homogeneous cells, are irregularly disposed, not uniform in height or shape, and vary from one to four, or rarely five, seriate. In the beginning of the growth ring the large vessels, or pores, as they are termed when viewed in cross section, are scattered and never more than two to three rows deep. In the remaining portion of the growth ring they may be either solitary or arranged in radial groups, usually of from two to three, or rarely five. Great variation is exhibited in the thickness of the vessel walls. The larger vessels in the early wood usually have comparatively thin walls with their lumina rather densely occluded by tylosal formations. The smaller vessels in the late wood as a rule have exceedingly thick walls, especially where contiguous. In general it may be stated that all solitary vessels have comparatively thin, uniform cell walls. The grouped vessels, however, usually have very thick walls which decrease in thickness characteristically at their distal ends. The walls of contact between two vessels bear densely packed and rather large bordered pits, the borders sometimes being hexagonal owing to crowding. Where they border on the medullary rays the walls of the vessels are furnished with simple pits. The scalariform markings characteristic of yellow birch and sugar maple woods are totally lacking in this one. Wood parenchyma occurs abundantly but is exceedingly variable as to its distribution. In trans-

verse section the individual cells of wood parenchyma resemble in general shape the fibrous elements, but have wider lumina by reason of their thinner walls. They predominate in the more porous parts of the growth rings and often closely surround the vessels. In the dense late wood, the wood parenchyma forms conspicuous, tangentially arranged bands alternating with irregular, compact rows of thick-walled wood fibers. On a perfectly smooth transverse section having well-defined late wood, these parenchyma bands can be detected with the unaided eye. When greatly interrupted by wood fibers the parenchyma bands become indistinct and can be distinguished only by means of a microscope.

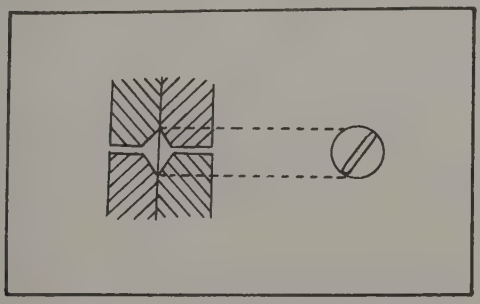

FIG. 6.

Bordered pit in butternut hickory (*Hicoria minima*) wood, transverse section, X 2,000.

As seen in longitudinal section the wood parenchyma cells extend vertically in short rows, the terminal cells of which taper to a point. Structurally they resemble the pith-ray cells but have their long axes at right angles to these. The individual cells of wood parenchyma are mostly short and prismatic, their thin walls being furnished with simple pits. Many of the individual cells contain solitary crystals of calcium oxalate belonging to the tetragonal crystal system. These crystals are only slightly soluble even in the strongest acids and are readily seen under the high power of the microscope in all sections. In such cases the whole cell becomes

merely a repository for the crystal and in so doing the walls usually become greatly distended. The wood prosenchyma elements compose the greater part of the dense outer portion of the annual growth ring and are relatively thick-walled. They have comparatively wide lumina and walls furnished with numerous small but distinct bordered pits, the orifice of which is slit-like and usually oblique (Fig. 6). These elements have a constant structure and in shape and size resemble wood fibers more than tracheids.

Microchemical Reactions of Normal Wood.— Cross sections of normal wood, when treated with chlorzinc-iodine, exhibit comparatively little of the characteristic violaceous coloration indicative of cellulose. The middle lamellæ of all the cells, the vessel walls, medullary ray cells, and the thin-walled wood parenchyma cells all color yellowish-brown. The wood prosenchyma elements exhibit a slight violaceous coloration which is strongest in the tertiary layer bordering on the cell lumen and fades off gradually toward the middle lamella of each cell. This violaceous coloration is most prominent in the springwood elements and diminishes in intensity toward the outer face of the growth ring at which point it is scarcely distinguishable. In sections treated with phloroglucin-HCl the thick vessel walls and the middle lamellæ of all of the cells color most strongly, these becoming dark rose-colored or wine-colored. The remaining layers of the medullary ray and wood parenchyma cells are found to be tinted less strongly but still much more so than the remaining layers of the wood prosenchyma elements which appear almost violet. After treatment with aniline-sulphate-H_2SO_4 the vessel walls and the middle lamellæ of all the cells exhibit a brilliant golden yellow coloration. The remaining layers of the medullary ray and wood parenchyma cells likewise become strongly colored, but assume more of a brownish-yellow instead of the golden-yellow color. The remaining layers of the wood prosenchyma elements stand out much less strongly than the middle lamellæ and appear to be of a pale lemon color.

From the tests described above in full detail, and from still other tests employed for the differentiation of both cellulose and lignin, it is evident that the vessel walls are by far the most strongly lignified of any of the elements. It is also evident that the medullary ray and wood parenchyma cells, while less strongly lignified than the vessel walls, are more strongly lignified than the wood prosenchyma elements. Of the individual cells the middle lamellæ are lignified to a much greater extent than their secondary layers of thickening. It is further evident that the secondary and tertiary layers of thickening of the prosenchyma elements are the least lignified tissues of the wood. As a result of the dissimilar structure and microchemical reactions of the various elements we naturally would expect to find that the vessel walls would resist decay longer than any other one element. Of the other elements the middle lamellæ would be more resistant to the solvent action of the fungus than the secondary layers of thickening possessed by these respective elements. It would therefore appear that the secondary layers of thickening possessed by the wood prosenchyma elements would decay most rapidly.

Macroscopic Appearance of Decayed Wood.— In its general features the macroscopic appearance of decayed bitternut hickory wood is essentially the same as that described for yellow birch. The last element to resist decay within the individual pockets was the vessels, which evidently were strongly lignified. In well-decayed wood the vessels, under a hand lens, appear as minute glass tubes lying loosely within the various pockets, all the other elements having disappeared long ago. In fact the wood was decayed to such an extent that the individual vessels could be removed readily with tweezers and used for microscopic study. Numerous mycelial strands, running both longitudinally and radially through the decayed wood, were readily visible to the unaided eye.

Microscopic Characters of Decayed Wood.— The dissolution and course of delignification of the woody elements is

essentially the same as that described for yellow birch. The various kinds of elements, however, decay in somewhat different order than in yellow birch, due to the entirely different structure of bitternut hickory wood.

Cross sections of well decayed bitternut hickory wood when treated with phloroglucin-HCl, present a very striking appearance. After staining with this reagent one is able to see clearly that the elements disappear in a definite order. The vessel walls take on an intense red-violet coloration even when remaining as almost isolated elements in a completely decayed mass. The cells immediately bordering the vessels likewise become colored deeply but the reddish-violet coloration is less intense than that exhibited by the vessel walls and diminishes rapidly in intensity so that a few cells away from the vessels this coloration is very slight or entirely lacking. Closer investigation, however, shows that the vessels usually are surrounded by a layer of wood parenchyma cells which, as will be shown later, also are very resistant to decay. Owing to this peculiarity and the fact that their walls were more intact it is apparent that the cells immediately adjoining the vessels are less susceptible to decay or at least decay more slowly than the more distant-lying elements. The pith-ray cells, as evidenced by the deep coloration acquired by their walls and their resistance to decay, are second only to the vessels in resisting decay. The pith-rays frequently remain in place with the cell-walls moderately intact and exhibit a good coloration with phloroglucin-HCl, while the elements on either side may be considerably disintegrated. The wood parenchyma cells are decayed before the pith-ray cells but remain intact much longer than the wood prosenchyma elements. Hickory wood, as explained earlier, is characterized by lines of wood parenchyma which extend tangentially between the pith-rays. In portions of decayed wood these two lines of elements can be seen remaining in a partially decayed state while the intervening spaces contain only the remnants of cells or may be entirely empty (Plate XXIV, Fig. 2).

In decayed wood treated with chlorzinc-iodine the lamellæ of the prosenchyma elements which remained colorless after treatment with lignin reagents were colored violet. The vessel walls, medullary ray cells, and wood parenchyma, as well as the middle lamellæ of the prosenchyma elements assumed a brownish-yellow tint, thus indicating that they were still lignified. The tertiary and secondary layers of the prosenchyma elements which fail to respond to lignin tests doubtlessly have been reduced to free cellulose, as evidenced by their violet coloration after treatment with chlorzinc-iodine. They remain in place until after all the cell-wall is delignified but the middle lamella. After all the layers of the cell-wall but the primary lamella have become delignified the destruction of the cellulose commences. As was seen to be the case in the decay of yellow birch wood, these cellulose layers frequently undergo a decided swelling upon the application of chlorzinc-iodine. The middle lamellæ of the prosenchyma elements remain in place and respond to tests for lignin not only until the tertiary and secondary walls have become delignified but even long after they have completely disappeared due to the dissolution of the cellulose remaining in them. In time, however, even the middle lamellæ become thinner and thinner until they break up into dissociated fragments. Even here microchemical tests show that the parts of the middle lamellæ which originally formed the cell corners, still respond to lignin tests while the other portions respond only to tests for cellulose.

In the earlier stages of the decay the hyphæ tend to extend themselves in the direction that offers the least resistance. As a result they are found to follow mainly the lumina of the various elements, especially those of the vessels. The vessel segments, however, are more or less occluded by tylosal formations which at first offer some resistance to the spread of the hyphæ. These tyloses, however, are comparatively thin and only serve to retard the spread of the hyphæ for a time as the fungal hyphæ soon dissolve their way through and continue their growth. In time the vessels often become filled with a dense growth of mycelium. As the decay prog-

resses the hyphæ quickly ramify and penetrate adjoining cells, soon extending in all directions throughout the woody tissue. They are comparatively small, rarely being over two microns wide, usually much less. Cross-walls and clamp connections are occasionally discernible in the larger hyphæ.

Careful examination was made of sections of decayed wood to determine the action of the fungal hyphæ on the crystals of calcium oxalate in the wood parenchyma cells. In no case could any solvent action be noted. In a number of instances, however, crystals were seen which remained intact after all the surrounding woody tissue had been completely dissolved away. The crystals, of course, were retained in their original position in the sections by the celloidin matrix in which the material was imbedded. It would seem from this circumstance that these crystals are not only of no use to the fungal hyphæ but are not capable of being reduced by their enzyme secretions.

As in the decay of sugar maple wood, longitudinal sections of decayed wood showed a matting of fungal hyphæ within the vessels, these hyphæ often being encrusted with brown decomposition products. Sections (taken near the black zones) of wood in the early stages of decay exhibited abundant brown gum-like masses of decomposition products occluding the lumina of the vessels and other elements.

The Decay of Chestnut Oak Wood.

Structure of the Normal Wood.— The wood of the chestnut oak (*Quercus prinus* Linn.) is heavy, hard, strong, tough, moderately close-grained, and durable in contact with the soil. The heartwood is yellowish or reddish brown and sharply defined from the lighter and slightly reddish, narrow sapwood.

Macroscopically the wood of chestnut oak presents the usual features of the ring-porous type, the pores abruptly diminishing in size from early to late wood. The larger pores contain abundant tyloses. The pores in the early wood are arranged in 3–5 rows and are conspicuously large; those in the late wood are minute and arranged in radial lines

branching toward the periphery of the growth ring. The pith-rays are exceedingly numerous and vary in size from those too small to see with the unaided eye to great broad ones.

Microscopically the wood of the chestnut oak is seen to consist of (a) both uniseriate and multiseriate pith-rays, (b) pitted vessels, (c) metatracheal zonate parenchyma with simple pits, and (d) wood prosenchyma of two distinct types, one having thin walls and bordered pits, and the other having thick walls and simple pits.[19] The pith-rays are exceedingly numerous and constitute about one-fifth of the cellular substance of the wood. Large pith-rays are often from twenty to thirty cells wide and from three to six times as high, and appear as long, well-defined lines in transverse sections. The pith-ray cells occur in from one to many rows closely packed together. Individually they are arranged end to end with their long axes in a radial direction. In a transverse section these radial rows of parenchyma cells appear as narrow but more or less distinct lines, the larger ones extending from the pith to the periphery of the stem. Where these cells are in contact with one another or with wood parenchyma fibers the pits are simple, but if they lie next to the vessels or tracheids the portion of the converging pits in the vessel walls is bordered, and that of the ray cells is simple.

The vessels or tracheæ make up chiefly the inner and more porous part of the growth ring. In the early wood they are round or elliptical and from 2–5 rows deep. Small vessels in the late wood are often polygonal and sometimes so small that their diameters hardly exceed those of the wood parenchyma elements. Radial rows of small vessels, which occur in the late wood, are wavy or slightly branched and surrounded by numerous wood parenchyma cells which often form narrow tangential bands. The vessels are composed of comparatively thin-walled tube-like segments arranged longitudinally end to end, the cavities of the vessels communicate

[19] The description of the anatomical structure of this wood is based partially upon that given by Sudworth and Mell (1911, pp. 15–21; 38–39).

directly with one another, the adjoining ends being more or less completely absorbed so that the rows of cells or vessel segments finally form long, continuous tubes. The segments of the large vessels are barrel-shaped. After the vessels lose their sap and the air in them is rarified, tyloses (very delicate partition-like walls) begin to form and block up the cavities, rendering the heartwood impervious, or nearly so, to the passage of fluids. Tyloses consist of parenchymatous tissue which has been forced out of the turgescent adjacent thin-walled pith-ray cells or wood-parenchyma fibers into the lumina or channels of the vessels.

The individual cells of wood-parenchyma resemble the pith-ray cells, but are grouped in vertical instead of horizontal rows. They predominate in the more porous parts of the annual rings and often closely surround the vessels and tracheids. In either case they remain extremely thin-walled. In the early wood they occur isolated or scattered. In the dense late wood, the wood parenchyma elements form conspicuous regular or branched and interrupted tangential bands which can be seen readily with the unaided eye. The pits are chiefly simple. Wood parenchyma cells usually contain starch and also a certain amount of tannin. The amount and nature of the contents of the parenchyma depends largely upon the age of the tree, the time of felling, and the part of the tree from which the wood was taken. Crystals of calcium oxalate are of common occurrence in all parenchymatous tissue. As in sugar maple wood they are developed singly in the cells and belong to the tetragonal crystal system. In contiguous pith-ray cells they often form rows of 3–6, while in the wood parenchyma fibers they occur in much longer rows, particularly in the early wood, and are technically known as idioblasts. In such cases the whole cell becomes merely a repository for the crystal. Both the wood and ray parenchyma cells of the material examined were packed full of large starch grains, varying in shape from globoid to ellipsoid.

As stated earlier, two kinds of wood prosenchyma are present — compactly arranged, thick-walled fibers and scat-

tered, thin-walled fibers. The former have occasional minute simple pits and are of the nature of typical wood fibers; the latter have numerous, more or less narrow, oblique bordered pits and resemble typical tracheids. The thick-walled wood prosenchyma elements are very fine, thread-like cells about 1.31 mm. long and 0.020 mm. wide. They occur in large compact groups alternating with the radial rows of more or less minute vessels of the late wood and are traversed radially by the uniseriate pith-rays and tangentially by irregular, more or less broken rows of wood parenchyma cells. The thin-walled wood prosenchyma elements occur scattered among the vessels, both the large vessels in the early wood and the radial rows of small ones in the late wood. (Plate XXV, Fig. 1.) The bordered pits in these prosenchyma elements are present irrespective of whether the contiguous elements are vessels, thick or thin-walled prosenchyma, or wood parenchyma cells. Except for the differences in the pitting of their walls, the thin-walled wood prosenchyma elements are essentially the same as the thick-walled ones. Tracheids are single fiber-like elements and are, therefore, easily distinguished from the vessels since the latter are formed by the fusion of cells placed end to end. In transverse sections, however, it is more difficult to separate them from the very small vessels.

Microchemical Reactions of Normal Wood.— Cross sections of normal wood, when treated with chlorzinc-iodine, exhibit comparatively little of the violaceous coloration indicative of cellulose. The large groups of thick-walled wood prosenchyma elements are the only elements to exhibit any appreciable violaceous color. The middle lamellæ of all the cells and the entire vessel walls are colored a golden brown. Both the secondary and tertiary lamellæ of the tracheids, the wood parenchyma and the ray parenchyma cells are colored a lighter brown than the middle lamellæ and exhibit little or no violaceous coloration. The ray parenchyma cells and the wood parenchyma fibers were very conspicuous after staining with chlorzinc-iodine, due to the

dark blue coloration taken on by the starch grains contained in these cells. In the areas of the growth ring occupied by large groups of thick-walled wood fibers both the secondary and tertiary lamellæ of these elements exhibited a light violaceous coloration. In sections treated with phloroglucin-HCl the walls of the large vessels and the multiseriate pith-ray cells are stained most strongly, becoming reddish violet. The middle lamellæ of all the cells also exhibit about the same degree of coloration; this is especially striking at the cell corners where the middle lamellæ often are thickened. The remaining layers of the small vessels, the cells of the uniseriate pith-rays, and the tracheids also become colored reddish-violet, but the coloration is much less intense than that exhibited by the walls of the large vessels. The secondary and tertiary layers of the wood fibers are colored still lighter, in fact, almost violet. The elements immediately surrounding the large vessels in the early wood of the growth ring frequently are colored almost as deeply as the vessel walls. After treatment with aniline sulphate-H_2SO_4 the walls of the large vessels and the multiseriate pith-rays take on a rich golden-yellow. The middle lamellæ of all the cells also are colored to the same extent and the coloration is especially striking at the cell corners. The remaining layers of the small vessels, the cells of the uniseriate pith-rays, and the tracheids also become strongly yellow-colored, but not nearly so much as the walls of the large vessels. The secondary and tertiary layers of the wood fibers turn only to a very pale yellow. The elements immediately surrounding the large vessels are colored almost as deeply as the vessel walls.

From the above tests described in full detail, and from still other tests employed for the differentiation of both cellulose and lignin, it is evident that the vessel walls and the cells of the multiseriate pith-rays are the most strongly lignified elements of the wood. Of the individual elements the middle lamellæ is the most strongly lignified layer. It is clear that the secondary and tertiary layers of the wood fibers are the least lignified portions of the wood. As a result of

the dissimilar structure and microchemical reactions of the various elements we would expect the multiseriate pith-rays to resist decay even longer than the comparatively thin-walled vessels. Of the individual elements the middle lamellæ would resist decay longer than the secondary layers of thickening of the respective elements. The least resistant layers would be the secondary and tertiary layers of the wood fibers.

Macroscopic Appearance of Decayed Wood.— The macroscopic appearance of decayed chestnut oak wood shows essentially the same type of decay that occurs in the other woods. Numerous fine black zones are to be seen in decayed trunks, when the decay has not progressed too far. Their occurrence is the same as in the other decayed woods described, namely, surrounding areas of undecayed wood and demarking them from the surrounding decayed wood. The black zones occurring in decaying chestnut oak (or other oak) wood usually are thinner and less conspicuous than those which predominately occur in the decay of most other dicotyledonous woods. The decayed wood examined was very friable but by no means in the last stages of decay. The pockets occurring in the decayed wood were somewhat inconspicuous owing to the heterogeneous structure of the wood. They were clearly visible, however, after the surface of the wood was moistened. Owing to the broad pith-rays of this wood its decay is quite comparable to that of sugar maple wood. The effect of the broad pith-rays in retarding the decay from spreading in any other than a radial direction is even more strongly exemplified in chestnut oak wood than that of sugar maple. The multiseriate pith-rays of chestnut oak wood are exceptionally thick, high, and broad, many of them extending unbroken from the pith to the bark. Unlike sugar maple wood, however, they do not lie so closely together. Nevertheless, they are important factors in forcing the decay to spread mainly in a radial direction, since, owing to their lignified nature, they are not attacked and penetrated nearly so readily as the other elements of the growth ring. As a result of this unequal spread of the fungus the decayed wood tends to rupture far easier in a

radial direction than in any other. In the more advanced stages of decay the broad medullary rays are still fairly sound and can be separated readily from the other elements which are considerably decayed. The numerous broad medullary rays which transverse the annual rings of growth serve to bind together the layers of growth so that there can be no separation along the line of the annual rings. In this way the medullary rays act as reinforcing structures so that the decayed wood responds far less to radial than to tangential compression. They likewise serve to increase materially the transverse breaking strength of the decayed wood. In consequence of the strengthening effect afforded by the medullary rays of this wood a trunk of chestnut (or any other) oak rotted by *Polyporus pargamenus* would resist breaking longer than those of most any other kind of wood decayed to a like extent by the same species of fungus.

Microscopic Characters of Decayed Wood.—The dissolution and course of the delignification of the woody elements is as near like that described for yellow birch wood as could be expected of a wood of such dissimilar structure. The thick-walled wood prosenchyma elements are the first to disappear and are closely followed by the thin-walled ones. After the disappearance of these elements the decayed wood appears skeletonized. At this stage of the decay the uniseriate pith-rays, the tangential rows of wood parenchyma cells, and the partially dissolved small vessels are still visible and are the only elements remaining within the intersections formed by the radially extending pith-rays and the tangential rows of wood parenchyma cells of the late wood. In this connection it may be mentioned that the late wood decays faster than the early wood of the annual ring, since the latter is composed mostly of large vessels surrounded by tracheids, both of these elements being highly lignified in this portion of the growth ring. Within the late wood of the growth ring the wood parenchyma cells are the next elements to disappear. By the time the parenchyma cells have disintegrated more or less completely the uniseriate pith-rays and the small vessels begin to break up. The large vessels in the

early wood of the growth ring remain fairly intact until practically all of the elements of the late wood have become considerably broken down. However, even these elements undergo digestion earlier than the occasional large multiseriate pith-rays. Even in thoroughly decayed wood these large pith-rays still remain hard and resistant, while the rest of the wood can be powdered readily by rubbing it between the fingers. It will be noticed here again that the elements in general disappear in a definite sequence which depends upon the degree of lignification exhibited by them. The individual cells of the multiseriate medullary rays probably are no more lignified than the large vessels, but their greater resistance to decay is to be attributed to the fact that they contain a greater mass of lignified tissue than do the vessels, and hence they are not penetrated so readily by the fungal hyphæ. Although the broad medullary rays do not occur so closely together as in sugar maple wood, they are much broader than the rays of the latter wood and would offer a very efficient barrier to the spread of the decay within the trunk in any other than a radial or perpendicular direction. The outermost rows of tangentially flattened cells in the growth ring are no more lignified than the other elements of the late wood and do not appear to resist decay any longer than the other elements. In the decay of sugar maple wood it will be remembered that the reverse circumstance occurred.

Longitudinal sections of decayed wood usually exhibit a great abundance of matted growths of hyphæ. In the later stages of the decay the network of resistant wood bounding the pockets largely disappears and in its place zones of matted fungal hyphæ occur, often forming a reticulum through the wood. (Plate XXV, Fig. 2.) The mats of hyphæ extend through the elements in all directions, crossing the vessels and even the large pith-rays. As a rule they are practically free from incrustations of brown decomposition products. As in the decay of sugar maple and bitternut hickory wood the fungal hyphæ apparently do not exert any solvent action upon the crystals of calcium oxalate commonly occurring in the wood parenchyma cells.

The Decay of Hemlock Wood.

Structure of the Normal Wood.—The wood of the hemlock [*Tsuga canadensis* (Linn.) Carr.] varies from light to medium weight, is soft, weak, stiff but brittle, coarse, and not durable in contact with the soil. The sapwood and heartwood are not well defined. The heartwood is but little darker than the sapwood; its color may be described as light brown with a slight reddish hue. The medullary rays are very fine, numerous, and inconspicuous to the unaided eye.

Microscopically the wood of the hemlock is of the nonporous type. Vessels are absent and the wood is composed of elements fairly uniform in structure. The contrast between the early and late wood is very decided, the transition frequently being abrupt. The growth rings are defined by the greater density of the late wood. Resin ducts normally are lacking. The wood consists of (a) uniseriate pith-rays; (b) tracheids with bordered pits, and (c) terminal wood parenchyma cells. The rays are numerous, distant 2–10 rows of tracheids, and vary from low to high. They are composed of two elements: (1) ray parenchyma cells with simple pits and (2) ray tracheids with bordered pits, the latter elements often interspersed, but mostly of marginal occurrence when viewed radially. According to Penhallow (1907, p. 267) the ray cells are somewhat contracted at the ends and average 3–5 spring tracheids in length. The upper and lower walls are very irregularly and often imperfectly, sometimes very sparingly, pitted. The terminal walls are not strongly pitted except in the summer wood. The lateral walls have small, oval pits, at first with a very narrow border which becomes more prominent toward the summer wood, the lenticular orifice becoming oblong; there are from 2–4, or in the summer wood from 1–2, pits per tracheid.

The wood tracheids in the spring wood are large and very thin-walled, conspicuously squarish or often elongated radially; furthermore, they are very uniform and in regular rows. In the summer wood they are more numerous, with thicker walls and smaller lumina, and in tangential section appear flattened, especially at the outer margin of the growth

ring. Bordered pits, either round or elliptical in 1–2 rows, more rarely in 1 row only, with large orifices, occur on the radial walls of the wood tracheids. According to Penhallow (*l. c.*) pits also occur on the tangential walls of the summer wood tracheids and are rather numerous, prominent, and flat. The resin cells or wood parenchyma cells (transverse section) are rather prominent, being more or less numerous on the outer face of the growth ring and rarely zonate. In addition the wood of hemlock normally is characterized by the absence of resin passages.

Microchemical Reactions of Normal Wood.— Normal hemlock wood treated with chlorzinc-iodine demonstrated the presence of comparatively little cellulose, most of the coloration being in the late wood. The entire cell-walls of the spring tracheids, the pith-ray cells, and the middle lamellæ of the summer wood tracheids exhibited a brown coloration. The tertiary and secondary lamellæ of the summer wood tracheids, however, did not color brown but exhibited a faint violaceous coloration. Evidently the reaction for cellulose was obscured by the presence of other substances within the cell-walls. In sections that had soaked for a time in a mixture of alcohol and glycerine the violet coloration exhibited by these layers of the cell-wall was far more pronounced. In sections treated with phloroglucin-HCl the middle lamellæ of all the cells were stained the strongest of all, becoming wine-colored. The remaining walls of the tracheids in the late wood colored deeply, but less strongly that the middle lamellæ; they colored to a deep reddish-violet. The secondary walls of the early wood tracheids assumed a somewhat lighter coloration. The cells of the medullary rays are very thin-walled and exhibit the same coloration as the tracheids of the early wood. After the treatment of sections with aniline sulphate-H_2SO_4 the middle lamellæ of all the cells again colored most strongly, becoming golden yellow. The remaining layers of the late wood tracheids likewise were colored golden yellow, but not quite so strongly as were the middle lamellæ. The golden

yellow color acquired by the late wood tracheids diminished in intensity in the tracheids of the early wood.

From the above tests described in full detail, and from still other tests employed for the differentiation of both cellulose and lignin, it is evident that of the individual cells the middle lamella is more strongly lignified than any other layer of the cell-wall. The tests employed indicate that the tracheids of the late wood are lignified to a much greater degree than the other elements of the growth ring. The medullary ray cells in the late wood apparently are no more strongly lignified than those in the early wood of the growth ring. From the dissimilar structure and microchemical reactions of the various elements we would expect the tracheids of the late wood to be far more resistant to decay than those of the early wood. The cells of the medullary rays of the wood examined responded strongly to the iodine test for starch, since the wood was cut late in the autumn.

Macroscopic Appearance of Decayed Wood.— As in the other woods studied the first evidence of decay is the occurrence in the wood of small irregular areas in which the tissues have lost their natural light brownish coloration and appear as though bleached. As the decay progresses it is evident that it is confined to numerous centers of activity, resulting in the formation of small pockets separated by narrow zones of wood which decay far less rapidly. At first the future pockets appear as bleached areas separated by a network of wood retaining its natural color. Within the individual pockets the decay progresses in a direction parallel to the woody elements, and in time the wood in these areas rapidly disintegrates and becomes pith-like. Even when the decay in the individual pockets is more or less complete the wood between the pockets is but little decayed so that it appears as a network of lines bounding the pockets.

The fungus usually begins to decay at the point of union of two growth rings. In hemlock wood the progress of the decay seems to be dependent upon the physical qualities of the woody tissue in the different portions of the growth ring.

In this wood the contrast between early and late wood is very decided. Consequently it is only natural that the decay should start between the annual rings where the soft spring wood adjoins the hard summer wood. Therefore, as the decay progresses we should expect to find the soft spring wood decaying far more rapidly than the harder summer wood. It is characteristic of the decay that the early wood, especially the innermost portion, becomes badly disintegrated and full of large pockets, while only the outermost surface of the late wood is attacked, and then only very superficial pockets appear. Thus we have an explanation of one of the most conspicuous features of the decay of hemlock wood by *Polyporus pargamenus* — the separation of the annual layers of growth in the early stages of the decay. Owing to the peculiar structure of this wood and the manner in which it is decayed by the fungus, it is only natural that it should separate along the line of the growth rings when subjected to any stress.

In the later stages of decay the wood becomes almost uniformly pith-like and full of conspicuous pockets of varying size. (Plate XXVI.) Within local areas of the wood disintegration often becomes so complete that a mere shell of wood of quite uniform thickness is all that separates the pockets from one another. The pockets are very variable in size, depending upon the extent to which they have united. The largest of the pockets rarely exceed 10 x 2 x 2 mm., extending in the wood in a direction parallel to the axis of growth. At this stage of the decay most of the pockets are entirely empty and free of any partially decomposed woody fibers and present a clean-cut appearance. Closely appressed to the inner walls of the pockets are numerous fine white strands of mycelium, which can be seen to best advantage in a longitudinal section of the wood. In addition larger white strands of mycelium frequently transverse the pockets at right angles (Plate XXVI), the same strand frequently extending through several pockets. At this stage of the decay the finer grained wood and wood of uniform and regular growth at least has a regular honeycombed appearance,

as shown by the transverse view. The separation of the wood along the line of union of the growth rings is now less conspicuous, for by this time it has become so thoroughly decayed that it tends to break in all directions with equal facility, although it still is far more resistant to transverse breakage than to breakage in any other direction.

At the beginning of the decay all the pockets originated on the inner face of the early wood. In the latter stages of the decay the unequal structure of the two portions of the annual ring is overcome, especially in trees in which this difficulty is not so pronounced, and the whole of the annual ring frequently is uniformly decayed. In general the decayed wood is characterized by a single zone of pockets occupying most of the annual ring, all of which lie well within their respective growth rings. In other words, the pockets are confined to the interior of each growth ring and do not occur with equal facility at the line of junction of two adjacent growth rings as is commonly the case in most of the dicotyledonous woods which have a far more uniform structure so far as the density of the elements in the early and late wood respectively is concerned.

In the very late stages of the decay, when the unequal structure of the two portions of the growth ring is overcome, the pockets, by the successive fusion of adjacent ones, may extend from one growth ring into the next so that the zonate arrangement of the pockets within each growth ring becomes entirely obscured. By this time many of the pockets have attained an unusually large size, some being 3.5 cm. or more long and 6 mm. or more broad. They are still highly irregular in outline and are separated by very thin, almost membrane-like layers of spongy wood. The larger pockets are free from contents and their walls appear clean cut and smooth save for numerous mycelial strands, most of the larger of which run radially in the wood. The remaining woody substance no longer presents a brownish and whitish mottled appearance, but the honeycombed wood now is of a uniform light brown color. This is due to the complete destruction of the partially disintegrated elements that

earlier remained in the pockets and gave them a whitish appearance. The remaining woody tissue is now very soft and sponge-like when wet; when dry it becomes somewhat stiffer and more brittle, but still retains much of the spongy texture.

The bark of the hemlock, on the other hand, is very resistant to decay and remains entirely sound, even though all of the sapwood immediately underlying it be reduced to pith-like consistency. Its extreme durability is due, in a large measure, to the high tannin content.

Comparison of the Decay of Hemlock Wood by Polyporus pargamenus and P. abietinus.— Earlier in this paper an effort was made to distinguish between the sporophores of *P. pargamenus* and its near relative, *P. abietinus*. The resemblance of the decay produced in hemlock by these respective fungi, however, is even more confusing than the resemblance between their sporophores. In hemlock wood of a more nearly uniform structure it has been noticed that *P. abietinus* sometimes begins to decay the late wood first. Whether this ever occurs in the decay caused by *P. pargamenus* the writer is unable to say. In other cases *P. abietinus* decays the early wood just as rapidly as the late wood, and in hemlock wood of a decidedly uneven texture the early wood is considerably decayed before the late wood of the annual ring is attacked appreciably. Hemlock wood decayed by *P. pargamenus* had numerous prominent white strands of mycelium running radially in the wood. In that decayed by *P. abietinus* the radially running white mycelial strands were even more abundant and conspicuous. Aside from these minor differences no other difference in the manner of the decay of hemlock wood by these two closely related fungi could be observed macroscopically.

Microscopic Appearance of the Decayed Wood.— From the microscopic appearance of the decayed wood it is evident that extensive chemical changes must have occurred to produce such great structural alterations of the woody substance. A comparison of cross sections of both normal and decayed

wood after treatment with various microchemical reagents reveals the action of the fungus.

In sections of decayed wood narrow, irregular zones of wood, in which the cell-walls respond to lignin tests as strongly as they do in normal wood, separate the pockets or decayed areas. Bordering on these cell-walls, which react the same as those of sound wood, are other cells in all stages of decomposition. The cell-walls of the decayed wood become colored variously, the coloration assumed corresponding with the degree of decay exhibited by the cell-walls. Those walls remaining but little or not at all decayed color the same as those in the sound wood. In other parts of the sections the tertiary layer — that portion of the cell-wall which borders upon the lumina of the cells — fails to take on the characteristic coloration or at least becomes stained only slightly, thus indicating the beginning of delignification. In other groups of cells both the tertiary and secondary layers of the cell-wall fail to take on the characteristic coloration to any appreciable extent. This indicates a more advanced stage of the decay and consequently the delignification.

The layers of the cell-walls that remained colorless after treatment with lignin reagents become colored violet when treated with cellulose reagents such as chlorzinc-iodine. In some cells only the tertiary lamella colors violet, the secondary and primary lamellæ becoming brown. In other cells only the middle lamella colors brown, both the secondary and tertiary layers becoming violet. Sections from a number of blocks of decayed wood were examined to see if any swelling of the cellulose layers occurred after treatment with chlorzinc-iodine. In the material examined, however, but little or no swelling of the delignified layers of the cell-wall could be detected after treatment with this reagent. The middle lamellæ retain their lignified nature long after the complete dissolution of the secondary and tertiary lamellæ of the respective cells. After the dissolution of the other layers of the cell-wall the middle lamellæ do not remain intact as long as those of yellow birch. Soon after the destruction of the tertiary and secondary layers the middle lamellæ

become broken up into dissociated fragments, among which the lignin reaction persists longest at the cell corners where the middle lamellæ are the thickest. In time, however, even these portions of the middle lamellæ become delignified and take on a pronounced violet coloration with chlorzinc-iodine.

Sections of decayed wood are stained permanently with aniline safranin and Delafield's hæmatoxylin and depict the occurrence of lignin and cellulose respectively within the cell-walls. In those cell-walls which are still comparatively free from decay the middle lamellæ stain a bright red while the secondary and tertiary lamellæ are paler. In adjoining cells where the tertiary lamella has been delignified this layer appears blue thus indicating the presence of free cellulose. In cell-walls that are still further decayed very little red (indicating lignified walls) appears and more blue (indicating free cellulose) appears on the inner portion of the cell-walls. Examination of cells immediately bordering on the empty pockets shows that the thickened corners of the middle lamellæ are the last elements to disappear under the action of the fungus. In portions of sections of decayed wood where a crumbled mass of fragments is all that remains of a group of elements, these thickened corners of the middle lamellæ may still be seen on account of their bright red color. In other parts of this mass of material consisting chiefly of dissociated remnants of the middle lamellæ it can be seen that the latter have taken on a blue coloration, thus indicating that even that portion of the cell-wall which originally was most strongly lignified ultimately has been reduced to free cellulose.

Sections were not made of hemlock wood in an early stage of decay where only the springwood was decayed and the harder summerwood remained normal. All of the wood studied microscopically was in the advanced stages of decay and had pockets distributed uniformly throughout the growth ring, each pocket being separated by irregular, narrow zones of less decayed wood. The medullary ray cells do not appear to be dissolved any quicker than the adjoining tracheids. In fact within any one pocket or center of decay all the ele-

ments disappear with approximately equal rapidity. In the earlier stages of the decay the hyphæ follow mainly the course of the tracheids and medullary rays. The lumina of the tracheids frequently become occluded by a dense growth of minute fungal hyphæ. By the time pockets have been formed in the wood the fungal hyphæ are found to be abundant in nearly all the woody elements, penetrating them in all directions and filling their walls with numerous perforations. The perforations made in the walls of the elements are exceedingly minute at first but continue to enlarge until they become many times their original size. The hyphæ frequently pass from one tracheid to another by means of the bordered pits on their radial walls. In such cases the entire pit — border and all — often is dissolved out entirely. The hyphæ found in decaying hemlock wood as a rule are so fine and minute that their morphological features necessarily are indistinguishable. Occasionally, however, larger hyphæ occur which lack protoplasmic contents and in which cross walls and clamp connections can be observed. In radial sections of decayed wood numerous mats of hyphæ may be seen extending across one or more tracheids, occluding the cell lumen of each tracheid. These wefts of hyphæ seem to be incrusted with a light brown substance — possibly certain by-products of decomposition.

Tests for lignified and cellulosic tissue agree with one another in that they show a gradual delignification of the cell-wall, commencing at the lumina of the cells and proceeding outward, the thickened corners of the primary lamellæ being the last elements to become delignified. The destruction of the cellulose follows closely after delignification — in fact so closely that but little free cellulose is left temporarily in the partially decomposed cell-walls. From the closeness with which the destruction of the cellulose follows delignification it is evident why the pockets found in hemlock wood in the latter stages of decay always are so clean-cut and free from partially decomposed woody material which, in the majority of decays, usually consists of free cellulose.

The Decay of Other Woods.

The foregoing five particular woods were selected on the basis of their structure as type woods for the study of the decay produced by *Polyporus pargamenus*. At the beginning of this part of the investigation it was thought that broader and more momentous conclusions could be drawn regarding the nature of the decay produced by this particular fungus if the study was made on a number of representative woods of as widely different structure as possible, rather than on a number of woods selected more for the convenience with which they could be obtained. At the same time the idea of working with species of wood of commercial value for lumber was not lost sight of. In view of this feeling, type woods were selected from each of the three commonly recognized groups of woods. Among the heterogeneous (dicotyledonous) or porous woods yellow birch and sugar maple were selected as representatives of the diffuse-porous group, while bitternut hickory and chestnut oak were selected as representatives of the ring-porous group. Among the homogeneous (coniferous) or non-porous class of woods hemlock was selected as the representative wood. As a matter of fact, the selection of hemlock was a necessity since, with one exception, it was the only coniferous wood found to serve as a host for this particular fungus.

The results secured from the study of these five woods were further supplemented by macroscopic studies on other woods, although only the five type woods were imbedded in celloidin and sectioned on the microtome. The macroscopic appearance of the decay of the following woods by *Polyporus pargamenus* was examined and found to be essentially the same as occurred in the five type woods that were studied in full detail: Butternut (*Juglans cinerea*), pignut hickory (*Hicoria glabra*), glaucous willow (*Salix discolor*), trembling aspen (*Populus tremuloides*), large-tooth aspen (*Populus grandidentata*), white birch (*Betula populifolia*), paper birch (*Betula papyrifera*), sweet birch (*Betula lenta*), river birch (*Betula nigra*), blue beech (*Carpinus caroliniana*),

chestnut (*Castanea dentata*), beech (*Fagus atropunicea*), white oak (*Quercus alba*), live oak (*Quercus virginiana*), red oak (*Quercus rubra*), scarlet oak (*Quercus coccinea*), yellow oak (*Quercus velutina*), pin oak (*Quercus palustris*), black jack oak (*Quercus marilandica*), willow oak (*Quercus phellos*), tulip-tree (*Liriodendron tulipifera*), sassafras (*Sassafras sassafras*), red gum (*Liquidambar styraciflua*), wild plum (*Prunus americana*), wild red cherry (*Prunus pennsylvanica*), black cherry (*Prunus serotina*), red maple (*Acer rubrum*), and striped maple (*Acer pennsylvanicum*).

Summary of the Physical and Chemical Changes in Decayed Wood.

Macroscopic Characters.— Cross sections of trunks of the four dicotyledonous woods studied here in full detail, as well as many of the other dicotyledonous woods studied only macroscopically, exhibit a number of conspicuous, irregular zones of black wood. These black zones are present invariably in the early stages of the decay of most dicotyledonous woods and often are prominent features of the decomposition. No such black zones, however, were present in decaying hemlock wood. A more detailed discussion of these black zones, in which their origin, physiologic significance, and chemical relationships will be considered, will later be taken up under the heading " The Metabolic Products of *Polyporus pargamenus.*"

The decays of the five woods of widely different structure selected for study here, all agree in their salient features. The first evidence of incipient decay is in the appearance of small, irregular areas in which the tissues have lost their natural color and appear as though bleached. These lighter areas are destined to become individual centers from each of which the decay spreads in all directions. The decay is at first localized or confined to these innumerable centers in which the destruction of the woody elements becomes completed before the decay spreads farther. As a result of the peculiar manner in which the decay acts the wood is decayed

unequally, the decayed wood appearing as light-colored areas while the less decayed wood lying between these areas still retains much of the normal color of the wood and appears on all three sections as a delicate network of lines. This network of less decayed wood usually is rather inconspicuous on the surface of dry wood but stands out quite prominently after the surface of the wood has been moistened. Even after moistening it sometimes still remains somewhat obscure in woods that possess very broad pith-rays, such as species of *Quercus*. In the course of time the elements within the individual centers for the spread of the decay become more or less completely disintegrated, while the thin zones of wood remaining between the decayed areas are still but little decayed. In general, excluding hemlock, all parts of the annual ring are equally susceptible to the attacks of the fungus. In hemlock, however, the decay originates in the soft early wood of the growth ring, the hard late wood not being attacked until much later.

As the solvent action of the fungus continues to progress the white, decayed areas continue to enlarge. Within the individual decayed areas the decay progresses mainly in a direction parallel to that of the woody elements. In the course of time the woody elements in these respective areas are reduced rapidly both in color and hardness until they become more or less pith-like. This method of decomposition results in the formation of innumerable pockets throughout the wood, these pockets being separated by thin, often almost membranous, layers of less decayed wood. In the intermediate stage of the decay numerous white strands of mycelium, running both longitudinally and radially through the wood, often can be seen with the unaided eye. The presence of these strands of mycelium, however, seems to be dependent upon the activity of the fungal hyphæ within the decayed wood. By the time the decay has progressed to this point the wood has lost all of its original characteristics of color, odor, hardness, and strength, and has become a bleached mass of pithy consistency. Standing trees frequently are broken off long before they become decayed to this extent.

This, however, depends largely upon the age of the tree, structure of the wood, and the durability of the heartwood of the attacked species.

In still later stages of the decomposition two or more adjoining decayed areas or pockets frequently coalesce into one so that the wood has a decided "pocketed" appearance. The individual pockets are highly irregular in outline and their size depends entirely upon the extent of the decay. The largest pockets observed were in yellow birch wood, where they attained a maximum size of three mm. in diameter and three cm. in length. In general the greatest dimension of the pockets occurs in the same direction that the woody elements extend; occasionally, however, it extends at right angles to them. In the later stages of the decay the individual pockets are quite empty of contents save for a few scattered tubular elements — the vessels. Owing to their greater lignification these elements are the last ones to disappear under the dissolving action of the fungus in most woods.

In woods with very broad pith-rays, such as the maples and oaks, the larger pith-rays outlast the vessels and are the last element to disintegrate under the dissolving action of the fungus. In those woods having such broad pith-rays the tendency to the formation of pockets is more or less retarded by the presence of these pith-rays which are very resistant to decay. The broad pith-rays possessed by both maple and oak offer exceptional resistance to the spread of the mycelium in any other than a radial or horizontal direction. In the late stages of the decay these broad pith-rays which transverse the annual rings of growth in a radial direction, serve to bind together the layers of growth so that there is no separation of the decayed wood along the line of the annual rings as usually occurs in those woods which lack the broad pith-rays. Woods possessing such broad pith-rays would tend to resist the decay produced by *Polyporus pargamenus* much longer than other woods which lack them. The former type of woods, when decayed while in use, would hold under the

strain imposed upon them much longer than would those woods which lack these reinforcing structures.

The outer, corky bark of all the trees studied (both microscopically and macroscopically) has proved to be exceedingly resistant to decay. This outer, corky bark frequently remains entirely sound and free from decay in many trees even after the inner bark and the underlying sapwood may be completely rotted. The great resistance of the outer bark of most trees to decay is to be attributed to the presence of tannins which are noted for their preservative qualities. The efficacy of intact and uninjured mature bark as a barrier to the entrance of parasitic fungi into the trunk cannot be too strongly emphasized. When the outer, corky bark has become injured, however, the inner fibrous bark is of no avail in keeping out the spores of wood-destroying fungi. As a matter of fact the exposed cambial layer, which is exceedingly rich in food materials, immediately affords a highly favorable environment for the germination and subsequent development of any fungous spores that may chance to lodge thereon. In attacked trees, especially felled ones, the rapidity with which the fungous mycelium spreads between the bark and the sapwood is nothing short of surprising. In the course of the decay of the inner bark pockets or cavities are produced in it similar to the ones found in the decaying sapwood.

Microscopic Characters.— Prepared slides of the decayed woods, when examined under the microscope, show up the pocket formations very clearly. The pockets containing wood elements in various stages of decomposition are separated from one another by irregular zones of less decayed wood, varying from a few to several cells wide. In sections of wood in an advanced stage of decay all stages of decomposition, from incipient delignification to the complete disappearance of the elements may be seen. In the central cells of such zones all three layers of the cell-wall of the elements respond to lignin tests as they do in normal wood. The cells bordering on these elements are in various stages of decom-

position. In some the tertiary layer no longer gives the characteristic color reactions when treated with various lignin reagents, but remain colorless. In other cells the secondary lamella of the cell-wall also remains colorless and undoubtedly consists of practically pure cellulose. As a general rule both the secondary and tertiary lamellæ remain in place until after all the cell-wall but the middle lamella becomes delignified. After all the layers of the cell-wall but the primary lamella have become delignified the destruction of the cellulose commences. Those layers of the cellulose walls which remained colorless after treatment with lignin reagents take on a pronounced violet color when treated with cellulose reagents, such as chlorzinc-iodine. Groups of these cells sometimes are seen in which the middle lamellæ are colored brown with chlorzinc-iodine, while the secondary and tertiary lamellæ are colored a deep violet and frequently exhibit a pronounced swelling. Occasionally these cellulose layers swell up to such an extent that the cell lumen is scarcely visible. In general the dissolution of the cellulose does not occur within any one cell until some time after its wall, excepting the middle lamella, has become completely delignified. Within the individual cell the cell corners, where the middle lamellæ often are thickened characteristically, respond the longest to tests for lignin. Owing to the great degree of lignification exhibited by the middle lamella it remains in place long after both the tertiary and secondary layers of the cell-wall have disappeared. After the secondary layers of thickening have been dissolved the resulting woody tissue has a skeletonized appearance. It has all the elements but their walls consist principally of the middle lamella, the other lamellæ having practically all been dissolved away. These middle lamellæ retain the nature of lignified walls and offer considerable resistance to further dissolution. They are the last part of the cell-wall to disappear and, as stated before, remain in place long after the other lamellæ have completely dissolved. However, they too gradually grow thinner and thinner until they break up into irregular fragments. It is not until the middle lamellæ have disintegrated

to this extent that they respond to the cellulose test with chlorzinc-iodine. The corners of the middle lamellæ, where they are thickest, are the last portions to disappear under the dissolving action of the fungus.

Within the individual pockets or decayed areas the various classes of elements disappear in a definite order, depending upon the thickness of their walls in conjunction with their degree of lignification. In general, in the dicotyledonous woods studied, the thick-walled but little lignified wood prosenchyma elements are the first to disappear. In the decay of yellow birch wood the uniseriate pith-rays sometimes disappear before the other elements. It is highly probable that, in the case of living trees at least, the rapidity with which the pith-rays are attacked and destroyed depends largely upon the time of year that the wood was attacked by the fungus. If a tree was attacked at a time when large amounts of reserve food was stored in the pith-ray cells, it is quite likely that the smaller medullary rays at least would be the first elements to be attacked and dissolved by the mycelium. After the wood prosenchyma elements have disappeared the next element to go usually is the uniseriate pith-rays. The order in which the other elements disappear is subject to considerable variation in the different woods. In those woods containing but scanty wood parenchyma this element disappears before the multiseriate pith-rays. In those woods containing well-developed wood parenchyma this element disappears simultaneously with the multiseriate pith-rays. In those woods having no very large pith-rays, such as yellow birch and bitternut hickory, the vessels are the last element to disappear within the individual pockets. In those which contain broad pith-rays, such as sugar maple and chestnut oak, the broad pith-rays resist decay longer than the vessels. In general it may be stated that the vessels resist decay longer than any other one element excepting the broad medullary rays. Where the vessels occurred in groups they frequently separated from one another before they became entirely dissolved. The vessel walls behave very similarly to the middle lamellæ; they are very uniformly lig-

nified throughout but at the same time they are lignified to a much greater extent than the middle lamellæ of the other elements. In the case of hemlock, however, most of the elements being uniform in structure, they decay at approximately the same rate.

The mycelium exhibited essentially the same relation to each of the woods studied. In the early stages of the decay of dicotyledonous woods the larger hyphæ tend to extend themselves in the direction that offers the least resistance. As a result of this tendency they extend longitudinally, following mainly the lumina of the various elements, particularly the vessels. When medullary rays are reached the hyphæ frequently branch off and enter them. The vessels often become filled with dense plugs or matted growths of fungal hyphæ. These mats of hyphæ are brown by reason of being incrusted with decomposition products. The latter are partially soluble in 5 per cent KOH and entirely soluble in warm nitric acid. In general the majority of the hyphæ elongate horizontally in the direction of the majority of the elements, during the earlier stages of the decay. In the later stages of the decay, however, the mycelium branches profusely and grows in all directions, perforating the walls of the woody elements at random. As the hyphæ continue to branch and multiply beyond the ordinary conception they permeate the woody substance in all directions and are thereby enabled to slowly dissolve the woody substance by means of their enzyme excretions. The hyphæ observed in the wood, as a general rule, are exceedingly fine and minute, rarely being over two microns wide and usually much less. Cross-walls and clamp connections are discernible occasionally in the larger hyphæ. In the course of the decay the hyphæ seem to disappear from the wood as soon as the decay of any one portion becomes completed. Numerous holes occur all through the wood indicating where the hyphæ had passed through the cell-walls. The threads exhibit no particular preference for the pits but penetrate the cell-walls at will. In those woods (sugar maple, bitternut hickory, and chestnut oak) which contain abundant crystals of calcium

oxalate, these crystals were found to be left perfectly intact after all of the surrounding woody substance was dissolved. From this observation it must be concluded that they are not only of no use to the fungal hyphæ but that they are not even capable of being dissolved by their enzyme excretions.

In all of the five woods studied in full detail it is evident that the first main chemical change brought about by the action of the fungal hyphæ is that of delignification. It is due to this action that the elements lose their natural brownish color and appear as though bleached. The results obtained indicate that the decay begins at the interior of the cell-wall and destroys the cell-wall progressively from the internal or last-formed lamella to the middle or primary lamella between two adjoining cells, first removing the lignin constituents. It is evident, furthermore, that delignification commences in the tertiary layer and proceeds outward toward the middle lamella or primary layer. After the cell-wall is delignified down to the middle lamella the reduction of the remaining cellulose layers then commences. After the destruction of the cellulose nothing is left but a skeletonized framework of middle lamellæ which in turn break up into fragments and undergo dissolution. Thus within a pocket or unit area of decay all stages of decomposition from incipient decay to final decay may be seen, all within the range of a few cells.

The results obtained from the above study of the decay by *Polyporus pargamenus* of five species of woods of such dissimilar structure are especially interesting in that they show a correlation between the structure of the wood and its detailed course of decay. The results obtained show clearly that the minor variations in the decay of different woods by this fungus are due to the dissimilar physical and chemical structure of the respective woods. In view of this fact it behooves us in describing the decay by any particular fungus not to draw too broad conclusions from the study of the decay of one or two species of woods when the fungus in question may attack a great number of species. To illustrate more specifically, it would not be advisable to conclude from the

study of the decay of one or two woods that the fungus destroys the pith-rays first, for example, since while such might be the case in woods with uniseriate or small pith-rays, the same course might not hold true in other woods possessing large multiseriate pith-rays. To my mind, in the past sufficient emphasis has not been laid upon the physical structure and chemical composition of wood when considering its decay by any particular fungus or when considering its predisposition to decay when subjected to known conditions under given uses. A knowledge of the chemical nature and physical structure of wood, however, has long been taken advantage of in connection with the preservative treatment of wood. In this connection a knowledge of both points would be of the utmost fundamental importance. For example, the Chicago, Burlington and Quincy Railroad has found by actual experimentation that it was not worth while to apply a preservative treatment to chestnut ties, since treated ties exhibited no greater resistance to decay and consequently no greater length of life in service than the untreated ones. The reason for this is that chestnut wood already contains a large amount of tannin which acts as a natural antiseptic or preservative and thereby retards the establishment and growth of wood-destroying fungi. Again, the abundance of tyloses in the vessels of the white oak group of woods has been found to render the wood very difficult to impregnate with preservative solutions. By reason of this peculiarity of structure, the woods of the white oak group are especially suitable for making liquid-tight containers (tight cooperage stock).

Localization of the Decay.

Undoubtedly the most peculiar and perplexing point in connection with the decay resulting from the action of *Polyporus pargamenus* is its habitual tendency to produce a minute, inconspicuous pocket type of decay. Unlike a great number of decays that produce a rot in which the entire mass of the wood is immediately affected, *Polyporus parga-*

nenus produces a type of decay in which the destructive changes at first are confined to localized areas of the wood but later spread so that the whole mass of the wood is soon involved. The pocket formation is not so pronounced at first in the earlier stages of the decay but becomes a conspicuous feature of the late stages as explained in the descriptions of the decay of individual woods. With the progress of the decay the destruction of the woody substance tends to be completed within the numerous individual pockets so that in the late stages of the decay practically no sound wood is left except the narrow zones separating the pockets. The pockets are not sharply defined until the late stages of the decay for in the intermediate stages they are more or less filled with a mass of partially reduced woody elements which remain in position next to the unchanged wood. In the late stages of the decay, however, the pockets frequently coalesce into larger ones separated by a mere membranous layer of resistant wood and become devoid of all contents save for a few vessel segments which resist decay unusually long. Microscopic sections of wood in this stage of decay show that the pockets are separated only by a thin zone of resistant wood from one to several cells wide (Plate XXIV, Figs. 1 and 2). This was especially marked in the sections studied in connection with the decay of yellow birch, bitternut hickory, and hemlock. In the sections of decayed sugar maple wood studied this resistant zone of wood was less pronounced and contained abundant masses of matted fungal hyphæ within the lumina of the elements of this resistant zone. In some of the sections of decayed chestnut oak wood studied the resistant zones of wood demarking the pockets had completely disappeared and in their place was left a reticulum or network of matted fungal hyphæ occupying the position formerly held by the resistant zones of wood. In fact suggestions of this transformation could be seen occasionally in certain sections of the other woods. In connection with the microscopic descriptions of the individual decays of the five woods studied in full detail mention was made of mats of hyphæ within the wood, particularly in the vessels, which

frequently were encrusted with brown decomposition products. The decay of the wood within the individual pockets was marked by a tendency toward an accumulation of decomposition products between the adjoining cavities. In this respect it is somewhat analogous to the decay of spruce by *Trametes pini* described by von Schrenk (1900[2], p. 33). In the latter decay, however, a distinct minute dark-brown zone, situated midway between two adjoining cavities, entirely surrounded the individual cavities. Von Schrenk states that a detailed examination of these dark-brown zones showed that they were due to masses of dark-brown hyphæ which filled each wood cell so as to completely occlude it, and that the hyphæ were encrusted with a brown substance which dissolves in part in dilute potassium hydroxide and entirely in warm nitric acid. The brown products encrusting the mats of hyphæ found in the decayed woods studied to determine the course of the decay caused by *Polyporus pargamenus* exhibited the same solubility tests as those enumerated by von Schrenk in the rot caused by *Trametes pini*. As von Schrenk (*l. c.*) observed, the brown encrusting substances occur in or on the cell-walls in the immediate vicinity of the pockets, and their manner of occurrence leads one to suspect that they were deposited in liquid form, for they have diffused through the various cells in all directions from the wall of the cavities.

As yet the causes which influence this local initiation of the physical and chemical changes, which is characteristic of several wood-destroying fungi, has not been determined. The decay of the light spots progresses rapidly until the wood becomes filled with distinct cavities or pockets. The hyphæ apparently branch out rapidly in all directions from each of the original centers of infection, and as they do so the metabolic by-products of decomposition likewise pass outward, passing along the woody elements faster than across them. After a period the advancing hyphal masses of two adjacent pockets meet in the narrow lamella of unchanged wood lying between the two unchanged pockets. By this time more or less of the brown substance representing decom-

position products has accumulated. This brown substance tends to occlude the lumina of the cells and collects in part on the fungal hyphæ and partly in and on the cell-walls so that these become brownish-black. As stated before, warm nitric acid removes these substances entirely, leaving the wood almost colorless. In the decay by *Polyporus pargamenus* of those woods studied there is only a slight accumulation of these partially decomposed substances midway between adjoining pockets. That this accumulation of the partially decomposed substances is not sufficiently great to arrest the decay at this point is shown by the anastomosing of adjacent pockets with one another in the later stages of the decay. It is evident, however, that even the slight accumulation of decomposition products midway between two adjoining pockets has a decided tendency to retard the advancement of the decay, since such infiltrated substances are more difficult for the fungus to assimilate than those constituents which have not been oxidized. Owing to this, the cell-walls of those cells, that have become infiltrated with by-products of the decomposition, which otherwise would be an important source of nutriment for the growth of the fungal hyphæ, have assumed through chemical decomposition a form more difficult to assimilate. On these grounds it is to be expected that the network of resistant wood left between the original centers of infection would be more resistant to decay than the centers of initial decay, owing to the tendency for resistant by-products of the decomposition to accumulate midway between the centers of initial decay.

The results obtained from the detailed study of the decay of five species of wood of dissimilar structure indicate that the decay may progress to a varying extent within different woods. Such a study requires the securing of abundant material so that sections may be made from each wood in all of its various stages of decay. While it is not claimed that all stages of the decays of each of the five different woods were studied, sufficient sections of each were included so that the general course of the decay of each of these woods could be ascertained. In the decay of yellow birch and bit-

ternut hickory the last stages of the decay were represented by membranous partitions of resistant wood separating the pockets. As seen microscopically the membranous layers of wood varied from one to several cells thick, and the elements often were full of matted hyphæ. Within the individual pockets practically nothing was left save for a few scattered, half-disintegrated vessels weakly held together by a few fungal hyphæ. Practically all of the woody substance, as well as the fungal hyphæ, had disappeared within the individual pockets (Plate XXIV, Figs. 1 and 2). In the decay of sugar maple wood the pocket formation was less pronounced than it was in either decayed yellow birch or bitternut hickory wood. In the sections studied the decayed wood was by no means reduced to the same extent as that just described for yellow birch and bitternut hickory, but the decay seemed to become completed before less of the woody substance was so completely destroyed. Microscopic examination showed a reticulum of resistant wood but it was much less conspicuous than that observed in either decayed yellow birch or bitternut hickory woods. The more lignified cells within the center of these zones often were stuffed with matted hyphæ as in the case of the decay of the two last-named woods. Within the less sharply demarked individual pockets considerable partially decayed material remained, including the multiseriate pith-rays, the vessels together with the cells immediately surrounding them, and the terminal zone of more lignified cells on the outer face of the growth ring (Plate XXIII, Fig. 2). It would appear, therefore, that the decay either does not progress so far in sugar maple as it does in yellow birch and bitternut hickory wood or that the localization of the decay into pockets is in time overcome before the decay becomes completed, after which the subsequent decay would progress uniformly and involve the whole of the remaining woody substance. In the decayed chestnut oak wood studied the pocket formation was inconspicuous. The woody substance had not disintegrated quite as far as it had in the decayed sugar maple wood studied. Microscopic sections exhibited a distinct reticulum bounding the pockets.

This reticulum contained very little resistant woody substance in most cases and consisted mostly of masses of intricately interwoven minute hyphæ. Within the individual pockets even more partially decayed woody substance remained than in the decayed sugar maple wood studied. It would appear either that the decay does not progress so far in chestnut oak as it does in sugar maple wood, or that the original localization of the decay into pockets is in time overcome before the decay becomes completed, after which the subsequent decay progresses uniformly and involves the whole of the remaining woody substance. From the results obtained it would seem that the decay continues to progress longer and to become more complete in certain woods than in others. This irregularity is determined apparently by the resultant of the action of the hyphæ of this particular fungus in conjunction with the inherent qualities of the wood attacked. In any event the last trace of the reticulum of resistant wood separating the pockets is found in the reticulum of matted hyphæ remaining at the same point aftr the reticulum of resistant wood is destroyed.

Just why the hyphæ should collect into zones at these points is not clear. We know that in general in the decay of wood by wood-destroying fungi but comparatively little or scanty mycelium is to be found in the much-decayed portions of wood. This peculiarity is clearly evident within the pockets produced by *Polyporus pargamenus* and is very striking in the last stages of the decay. In the study of most any wood-destroying fungus one can almost always observe numerous perforations of the cell membranes in which the fungal hyphæ no longer are present. In the course of the progress of the decay the hyphæ branch and rebranch until they permeate all of the woody elements. It is not to be supposed that all of this increasing volume of fungal mycelium functions in the decay of wood but that it is mainly the minute, last-formed hyphæ that are active in secreting enzymes which gradually render the woody substance soluble and capable of absorption and translocation by the fungus. It is evident, from the habitual disappear-

ance of most of the mycelium within the wood upon the completion of the decay within any one portion, that the older mycelium has served its purpose, ceased to function and disappears, doubtlessly being dissolved by the enzyme excretions from the younger active hyphæ. We know that the membranes of fungal hyphæ consist of cellulose as a fundamental substance, its detection being rendered difficult by the presence of infiltrated substances, possibly of a protein nature. As evidence of cellulose constituting the basis of fungal membranes, we find that young fungal hyphæ in decaying wood frequently color violet with cellulose reagents instead of yellow or brown as do the older ones. When we consider that the chemical composition of the membranes of the fungal hyphæ is not so unlike that of woody membranes, it seems quite likely that the non-functioning hyphæ, under certain conditions, may be digested either by closely related or possibly the very same kind of enzymes which they formerly secreted to effect the dissolution of the surrounding woody membranes. If such procedure occurred within decaying wood, it is conceivable that, after a time, we might have a dissolution of the hyphæ which, in this case, might be most complete within the individual pockets and be retarded at the boundary between two adjacent pockets just as was the case in the decay of the woody elements. In this way we might account for the final reticulum of matted fungal hyphæ left surrounding the individual pockets where early in the course of the decay they were demarked by resistant zones of wood forming a reticulum at the same points which later come to be occupied by the reticulum of matted hyphæ.

The Metabolic Products of Polyporus Pargamenus.

Enzyme Activity in Polyporus Pargamenus.— From the anatomical and microchemical studies of various woods undergoing decay through the agency of *Polyporus pargamenus* evidence was obtained that several enzymes are secreted by the vegetative mycelium of this fungus. Thus the disappearance of starch, proteids, pectic bodies, cellulose,

and lignin constituents from the wood indicates that the mycelium produces diastatic, proteolytic, and a number of cyto-hydrolytic enzymes, among which are pectinase, cellulase, and ligninase. Aside from the histological methods employed in the study of the decay of these woods, no specific methods were employed for the detection of enzymes.[20]

The Black Zones Formed in Decaying Wood.— Undoubtedly the by-products most frequently met with in decaying wood are the extremely chemically resistant brown humic products which infiltrate portions of the wood, causing them to appear as brownish discolored areas, or which more often collect in narrow zones between the decayed and undecayed portions, causing the wood at this point to appear as a blackish zone or line or varying thickness. (Plate XXVII.) As shown by the writer (1917[2]) in an earlier publication dealing exclusively with the study of the black zones formed by wood-destroying fungi,[21] these formations, limiting various stages of the decay, are characteristic features of the early stages of the decay of dicotyledonous woods by wood-destroying fungi. These zones may extend in any direction through the wood or bark, their courses being determined by the initial starting point of the fungus and its subsequent growth and advancement through the wood. Their occurrence may be observed best on cross sections of a tree or log that is but partially decayed. Here they usually appear as irregular black or brownish-black lines of varying thickness, which occur between areas of wood in different stages of decay, either demarking decayed from undecayed wood or else demarking adjacent portions of wood that are in different stages of decay. Strictly speaking, the term "lines" should not be applied to these formations unless done in

[20] In planning the ground to be covered by the present investigation it was not considered advisable to lay any particular stress on the qualitative and quantitative determination of enzymes, since, although of fundamental importance, work of this kind is of such specialized nature that it falls more nearly within the domain of the physiological chemist, by whom it can best be done.

[21] Portions of this study dealt particularly with the black zones formed in wood decayed by *Polyporus pargamenus.*

describing their appearance in a section of wood. In reality they are thin zones of discolored wood which at first sharply separate the various stages of decay in the wood. If, however, the decay starts from several centers the dark zones extend very irregularly throughout the whole mass. Longitudinal sections of trunks in the early stages of decay show that these blackish zones extend for varying distances up and down the stem, their general course being parallel to the elements of growth. Their course, however, is in no way influenced by the annual rings of growth, but only by the progress of the decay effected by the fungal hyphæ; they may cross and recross the growth rings repeatedly.

These blackish zones are not constant in position, since the decomposition products which cause the discoloration move forward with the advance of the decay in any part of the stem and ultimately disappear upon its completion within that part. The continual occurrence of the blackish zones between decayed and undecayed wood is due to the fact that the decomposition products are destroyed, together with the wood containing them, while new ones are formed constantly from the sound wood as fast as it is attacked by the advancing mycelium.

The prominent blackish zones which are such characteristic features so commonly associated with many of the decays of deciduous woods are of rare occurrence in decaying coniferous woods. Similar formations are characteristic of various decays of coniferous woods, but they are inconspicuous when compared to the broad zones of decomposition products which commonly occur in the decay of dicotyledonous woods. Such decomposition products arising through the decay of coniferous woods by wood-destroying fungi, although of common occurrence, apparently are small in quantity compared with those arising through the decay of dicotyledonous woods. Such being the case, this difference must be attributed to the inherently dissimilar character of these respective groups of woods.

Macroscopic examination shows that these discolored zones are composed of wood of unusual hardness. Microscopic

examination shows that they are caused by brown infiltrations in the cell-walls and lumina of the cells, these infiltrations often becoming so abundant that they exude into the lumina of the cells, particularly the vessels, and occlude these completely. (Plate XXVIII, Figs. 1 and 2, and Plate XXIX.) This brown substance usually collects in a blackish zone or layer between two adjoining areas in different stages of decay. If it should happen that for some reason the progress of the decay be indefinite and retarded the brown product may appear merely as an unlocalized brown discoloration in the wood. When seen in mass it is responsible for the dark coloration mentioned above. At the time of its formation the brown product is a liquid, but, upon further decomposition, it changes to a brown, amorphous brittle substance, frequently becoming more or less cracked after dessication.

Chemical Origin of the Brown Decomposition Product.— The physical appearance and chemical composition of the brown by-product of decomposition varies greatly according to the extent to which it has become chemically altered. In the earlier stages of the decay much of this decomposition product is soluble in and can be extracted from finely divided wood with a 5 per cent solution of potassium hydroxide. If the potash solution be neutralized with dilute hydrochloric acid a reddish-brown gelatinous precipitate of humic acid is formed slowly, which gradually settles to the bottom. When dried the residue resembles the brown masses seen in many of the wood elements. Von Schrenk (1900[2], p. 37) describes the decomposition product as follows: "In mass it is reddish-brown, soft, tasteless and odorless, insoluble in alcohol, ether, chloroform, acetone, turpentine, etc., but very soluble in alkalies, KOH, $NaHPO_4$, etc., and can be reprecipitated from such solutions by acids." Because of its peculiar physical and chemical properties the substance has been classed among the "humus compounds." As was stated earlier in connection with the description of the decay of individual woods by *Polyporus pargamenus*, the hyphae fre-

quently are coated with a thin layer of this compound, so that their walls look brown and show several contour lines. The accumulation of this brown product signifies the first step in the decomposition of wood, and numerous investigations have shown that wherever there is any sign of decomposition this product appears immediately. Its formation appears to be associated with starch-containing cells, and for this reason it is most conspicuously developed in the pith-ray and wood parenchyma cells, these cells in the living wood having been largely concerned in the storage and conduction of food in the wood.

In the later stages of the decay the brown decomposition products appear to become further changed and more resistant to the action of chemical reagents. In this more resistant condition the brown decomposition product is mostly insoluble in alkalies and apparently can be brought into solution only by the use of powerful oxidizing agents, such as nitric acid or a mixture of hydrochloric acid and potassium chlorate. Such powerful reagents must necessarily change the nature of the substance under consideration. In a previous paper the writer (1917[2]) has reported the results of the analysis of the infiltrated substance giving rise to the black zones formed in wood decayed by *Polyporus pargamenus*. As much of the results as deal with the present problem will be included in this discussion. The subject for experimentation was a log of pignut hickory [*Hicoria glabra* (Mill.) Britton] exhibiting an advanced sap-rot resulting from the decay caused by *Polyporus pargamenus*. The thick corky bark of the log had proved to be very resistant to decay and remained of normal hardness. The thick sap-wood underlying the bark was almost completely destroyed save for a few isolated, small resistant areas of wood which were surrounded by conspicuous, thick, black zones, due to the accumulation of decomposition products at this point. A number of these resistant areas of the sapwood were removed and scraped free of the surrounding completely decayed sapwood, which was of pith-like consistency (Plate XXVII), and used for chemical analysis. The heart-

wood of the log, to all purposes, was sound and comparatively free from decay. It was evident that the fungus had subsisted upon the sapwood of the log for a period of years and that it had died out upon the completion of the decay of the sapwood.

Radial sections (10 microns), made of peripheral portions of these resistant zones of wood, exhibited an abundant accumulation of the brown decomposition products. The walls of the woody elements traversed by the peripheral black zone were browned; the pith-ray cells contained abundant brown drops, and the lumina of many of the cells were occluded by accumulations of the brown decomposition product. Farther within the resistant zones of wood, the cell-walls were free from the brown coloration, but practically all of the pith-rays contained abundant brown drops of humic products within their cells. All stages in the formation of this decomposition product were present from recently formed droplets to those which had coalesced to form gum-like masses which completely occluded the cell lumina. (Plate XXVIII, Figs. 1 and 2.) The wood evidently was in the first stage of decay, that is, it had been penetrated by fungal hyphæ, but its disintegration had not commenced.

A series of radial sections were cut from the material described and employed to determine microchemically the solubility of these decomposition products. The solubility tests were made by exposing ten micron sections to the action of the reagent (without heating) in watch glasses, meanwhile making observations with the microscope. If the numerous globules of the humic products, which were readily visible in the pith-ray cells under the low power of the microscope, did not dissolve after a reasonable length of time a small quantity of the reagent and sections were transferred to a test tube, heated to the boiling point, emptied out into a watch glass, and again examined under the microscope. The globules of humic products were found to be insoluble in water, concentrated ammonium hydroxide, 10 per cent solution of sodium hydroxide, 10 per cent solution of potas-

sium hydroxide, and concentrated hydrochloric acid. In cold concentrated sulphuric acid the wood was carbonized but the globules remained intact. Upon heating the acid to boiling the wood dissolved together with more or less of the humic products. In cold concentrated nitric acid the decomposition products were insoluble, but upon heating to boiling the globules dissolved together with the wood, forming a brown solution. Moreover, tests performed with other sections indicated that the decomposition products in question were insoluble in absolute alcohol, xylene, acetone, ether, petroleum ether, chloroform, carbon bisulphide, and carbon tetrachloride. In addition to this, sections of the wood containing the globules of humic products were placed in a concentrated solution of chloral hydrate and kept at a temperature of 55 degrees C. for one week. There was no effect other than a slight swelling of the globules. The same sections were then washed in water and dehydrated by alcohol. Part of them were treated with clove oil and the remainder with cedar oil, but the humic products remained insoluble in both cases.

An attempt was made to determine more fully the chemical nature of the brown decomposition product by means of a comparative analysis of sound and decayed wood. The resistant areas of sapwood removed from the pignut hickory [*Hicoria glabra* (Mill.) Britton] log were again employed for the study of the decayed wood, and sapwood (gathered in the spring) from a living tree of the same species was employed for the study of the sound wood. In the case of the resistant areas of sapwood in the early stages of the decay the periphery of each piece was bounded by a conspicuous thick, black layer of infiltrated wood as described earlier. The external black layer sharply demarked the completely decayed wood from the remaining resistant areas which were only in the first stage of decomposition. This black layer, as well as the wood enclosed by it, was very hard. The infiltrated wood was shaved off carefully, care being taken not to include the underlying, uninfiltrated wood. The normal sapwood also was reduced to shavings, and, after thorough drying, both samples were ground finely.

These samples of finely divided wood were first successively submitted to a preliminary extraction, without heating, for twenty-four hours with ether, 95 per cent alcohol, a 10 per cent solution of sodium hydroxide, and a 5 per cent solution of hydrochloric acid so that, when the dominant decomposition products were extracted finally they would be free from many extraneous substances. Parallel tests were conducted on equal quantities of infiltrated wood and of the normal sapwood. The ethereal and alcoholic filtrates, in both cases, contained such exceedingly small amounts of substance that they were not further investigated. The alkaline filtrate from the sound wood residue, upon the addition of 90 per cent alcohol, gave a characteristic precipitate of xylan (wood gum). The alkaline filtrate from the infiltrated wood, however, upon the addition of 90 per cent alcohol, gave a brown flocculent precipitate which, judging from its solubility and other chemical reactions, consisted mainly of the group of humic substances known as humic acid. After the alkaline extraction the woody residues were washed and then subjected to extraction with a 5 per cent solution of hydrochloric acid for twenty-four hours. The acid filtrates thus obtained were practically colorless and the woody residues, in both cases, apparently remained unchanged. After this extraction the one from the infiltrated wood was, as far as could be determined by microscopic examination, as darkly colored as it was at the beginning of the original treatment.

Both the woody residues were then subjected to the action of an oxidizing agent (hydrochloric acid and potassium chlorate), after which, according to Frank (1884) and Temme (1885), the decomposition products are rendered soluble in alcohol. Münch (1910), however, considers that Frank and Temme are in error for giving this reaction (alcohol solubility after digestion with hydrochloric acid and potassium chlorate) as a characteristic of wound gum, as they had termed the decomposition product, and shows that starch-containing cells which do not exhibit the slightest browning or gum formation likewise respond to this reaction. These authors, however, did not continue to investigate the

chemical nature of the brown decomposition product beyond finding that it was soluble in alcohol after digestion with a mixture of hydrochloric acid and potassium chlorate. This has been one of the chief objects of the present study.

Both of the residues were digested by boiling in a mixture of hydrochloric acid and potassium chlorate (5 gms. of potassium chlorate to 100 cc. of 80 per cent hydrochloric acid) for fifteen minutes. The woody residues from this oxidizing treatment, after thorough washing, were compared. It was found that neither was destroyed by the strong oxidizing action, but the residue from the infiltrated wood had lost all of its original blackish color and was only slightly darker than that from the sound wood. When examined under the microscope the cells of the ground infiltrated wood appeared to be filled with a light, reddish brown substance, while the cells of the sound wood also appeared to contain a similar substance but in smaller quantity. Both the oxidizing liquors left from this treatment were brown in color and when neutralized with sodium hydroxide gave brown precipitates respectively, the one in the case of the sound wood being the darker. These precipitates in both cases undoubtedly represent additional humic acid, the formation of which was rendered possible by the decomposition of humic substances resulting from the digestion of the woody substance with the hydrochloric acid-potassium chlorate mixture. Since they did not represent the main product to be studied, their investigation was not carried further.

The woody residues left from the oxidizing treatment were then submitted to a cold extraction with absolute alcohol for twenty-four hours. In both cases the alcohol instantly assumed a brown hue due to material entering into solution. This treatment seemed to take most of the coloring substance from both woods, although the residues responded slightly to a second and even to a third extraction. The alcoholic filtrates were evaporated to dryness and weighed. Roughly estimated, about twice as much material was obtained from the infiltrated wood as from the sound wood. Both extracts were dark brown in color and exhibited a vitreous fracture.

The one from the infiltrated wood was of the deeper hue. A small quantity of each extract when heated upon a platinum wire burned readily with a pale yellowish flame, emitting small quantities of a whitish vapor and giving off odors apparently peculiar to these substances. The extract from the infiltrated wood, when burned upon a platinum wire, left a dark brown, bead-like residue, while the extract from the sound wood, when treated in like manner, burned completely.

Both alcoholic extracts were insoluble in cold or boiling water, concentrated hydrochloric acid, ether, petroleum ether, chloroform, carbon bisulphide, and carbon tetrachloride. Their specific gravities are indicated by the fact that they were not suspended in or floated upon any of the organic solvents tried, of which the heaviest, carbon tetrachloride, has a specific gravity of 1.63. Neither, however, sank in concentrated sulphuric acid, whose specific gravity is 1.84. Both alcoholic extracts, however, were soluble in cold absolute alcohol, acetone, and a 10 per cent solution of sodium hydroxide. When the last-named solution was neutralized with sulphuric acid the extracts, in both cases, were precipitated — that is to say, they were insoluble in the exactly neutral sodium sulphate solution thus prepared. Both alcoholic extracts were soluble to a brown solution, but dissolved more slowly and without carbonization, when shaken in cold concentrated sulphuric acid. The alcoholic extract from the infiltrated wood was soluble in cold ammonium hydroxide, whereas that from the sound wood was soluble only by heating the reagent to boiling. When hydrochloric acid was added to the ammoniacal solutions until they were slightly acid both extracts were precipitated, leaving the solutions colorless in both cases.

None of the treatments thus far applied have secured a separation of the substances peculiar to the infiltrated wood and giving to it its distinguishing color. The solubilities and other properties of the respective extracts from the decayed wood indicate that a portion of the carbohydrate substance, particularly the hemicellulose xylan, had been converted into humic substances of two principal groups: First,

a relatively small amount of humic acid as represented by the humic substance soluble in alkali and precipitated from the alkaline solution by alcohol; second, a much larger quantity of humin as represented by the great majority of the brown decomposition product insoluble in alkali until after the digestion with a mixture of hydrochloric acid and potassium chlorate, by which it was transformed into soluble humic acid. The solubilities and other properties of the respective extracts from the sound wood in which all of the normal carbohydrate substance was present indicate that the humic substance originated from boiling the carbohydrate substance (minus the hemicellulose, xylan) with a strong solution of hydrochloric acid and potassium chlorate.[22]

As much of the results of the writer's previous work (1917[2]) upon the black zones formed by wood-destroying fungi as deals with the decomposition products formed by *Polyporus pargamenus* has been summarized as follows:

(1) The brown decomposition products formed in the decay of dicotyledonous woods infiltrate the cell-walls to a greater or less extent, frequently becoming so abundant as to form numerous brown drops within the lumina of the cells. Such deposits appear in the wood as blackish zones of varying thickness which occur at first between decayed and undecayed areas and later separate areas in different stages of decay.

(2) The blackish zones are not constant in position since the decomposition products which cause the discoloration move forward with the advance of the decay in any part of the stem and ultimately disappear upon its completion within that part. The continual occurrence of the blackish zones between decayed and undecayed wood is due to the fact that the decomposition products are destroyed by the advancing fungus together with the wood while new ones are formed

[22] It is well known that other carbohydrates may also yield humic bodies. For instance sugars on boiling with a number of mineral or organic acids artificially yield mixtures of humic acid and humin bodies, varying in proportion with the different sugars used.

onstantly from the wood as fast as it is attacked by the dvancing fungus.

(3) In the decay of coniferous woods the formation of umic substances similar to those studied here is very small n quantity as compared with those arising in the decay of icotyledonous woods.

(4) In wood free from fungous attack the formation of he brown decomposition products is dependent mainly upon he concurrence of three factors: (a) the presence of dead ells, (b) an optimum supply of moisture, and (c) a supply f oxygen sufficient to promote oxidation.

(5) The partially decomposed material of woody plants orms a particularly vague and indefinite group of substances containing all the non-volatile products of fungal, nzymic, and oxidative actions on the plant residues. The esultant humic substances are exceptionally resistant to hemical reagents.

(6) It is evident that the cell contents and certain other ubstances, particularly the hemicellulose, xylan (wood um), that originally were combined with the cellulose to onstitute the cell-wall furnish the formative material which, hrough oxidation upon the entrance of air and the presence f water, coagulates to thick drops and gives rise to the ecomposition products which ultimately infiltrate certain ortions of the wood, causing them to appear as blackish ones.

(7) In the wood of the pignut hickory the hemicellulose, ylan, is destroyed early in the progress of the decay. In the arly stages of the decomposition of the wood the wood gum pparently is the substance which gives rise to most of the umic substance.

(8) By the action of a strong oxidizing reagent on fresh apwood a brown humic substance can be prepared artiicially, which is essentially like that occurring naturally in icotyledonous woods, whether in wounded areas of living rees, dead wood, or as the result of their decay by *Polyporus argamenus* and other wood-rotting fungi.

(9) The properties of the extracts obtained respectively from sound and decayed hickory wood indicate that, in the course of the decomposition, a portion of the carbohydrate substance, particularly the hemicellulose xylan, becomes converted into humic substances of two principal groups, namely, humic acid and humin. It is the accumulation of these humic substances which gives rise to the dark brown decomposition products which are of such common occurrence in decaying wood.

(10) Humic acid and humin were produced artificially from the carbohydrate substance of the sound hickory wood by boiling with a mixture of strong hydrochloric acid and potassium chlorate. The substances thus produced indicate close relationship with the humin-like decomposition products formed as black zones in decaying wood.

(11) The chemically resistant by-products, often forming blackish zones in wood decayed by *Polyporus pargamenus*, have proved to be a group of substances analogous to or nearly identical with those substances concerned in the brownish discolorations in dead wood that is entirely free from fungous attack. The formation of the brown decomposition products in the latter case likewise is a sign of the humification which gradually sets in when the cell contents become dessicated or when their walls or contents undergo decomposition. This humification is greatly accelerated by the presence of wood-rotting fungi which greatly hasten the decomposition.

Chemical Affinity of the Brown Decomposition Product.— Now that the source of the decomposition product has been indicated, it is advisable to consider its final chemical nature. In the discussion of the chemical composition of the cell-wall the elaboration of those changes of tissue substances — celluloses and compound celluloses — which accompany or follow the cessation of vital activity has been deferred purposely until this point. It is more difficult to apply the term "death" to the vegetable than to the animal organism. In the sense of the elaboration of

new material, the active life in a perennial plant is linked only with structural portions. In a forest tree, for example, the leaves are these active agents; the tissues of the trunk, on the other hand, are largely depleted of the organic nitrogenous matter (protoplasm) upon which the vital activity depends. They have ceased to live in the strict sense of the term, but, on the other hand, they are known by casual observation to live in the sense opposed to decay. While there are various phases of life in the plant recognized by ordinary observation, and more exactly defined by the physiologist, these phases pass by insensible gradations to the point where decay and chemical disintegration are predominant. The most striking general feature of the cellulosic group is that its members are non-nitrogenous. It might be reasoned, therefore, that from the very first they are excreta and never live in the strict sense of the wood. We may conclude that, from the moment of origin, the history of the cellulose group is one of progressive withdrawal from the realm of the main vital processes, and that to re-enter that realm they must undergo a process of proximate resolution as a result of external action. This reabsorption of cellulosic tissues is a frequent phenomenon. The process by which the tissues become broken down is of the character of an ordinary hydrolysis, that is, it is determined by enzymes.

The writer has endeavored to trace the changes and modifications which these substances undergo in the normal life of the plant, and evidence has been given showing them to be highly reactive and susceptible of modification in various directions. He now wishes to follow the fate of these substances in the ordinary processes of the natural world. Under these processes "death" is succeeded by a variety of processes of decay and disintegration. They are in part intrinsic and in part determined by external agencies. They are of two kinds — processes of resolution and processes of combination or condensation — which usually are concurrent. The former are attended with evolution of gaseous products; the latter are defined by an extended series of their products, through all stages from "humus" to the coals. The chief

characteristic of this series of degradation products of plant tissues is the accumulation of carbon at the expense of ogygen and hydrogen.

The group of indefinite and complex organic substances formed in the decay of vegetable and animal matter are normal constituents of all soils and fulfill important functions therein. The resulting compounds may be those that were in the living tissues and have resisted decay, those that result from a splitting or degradation of complex bodies in the living plant, or compounds arising through changes brought about by micro-organisms, and nearly all classes of organic compounds known may be represented. These products have been classed under the general term "humus",[23] and so long as the term is used in a collective sense it may be retained as a convenient term.

The brown humus substances must be considered as a mixture of closely related bodies with and without nitrogen. These various substances have been divided into a number of groups by different writers, the subgrouping depending upon the solubilities of the substances. Schreiner and Shorey (1910) have grouped the various compounds they have isolated from the organic matter of soils as follows:

Extract soil with alkali

Alkaline solution, acidify		Insoluble
Acid filtrate	Precipitate, boil with alcohol	
Crenic Acid	Humic Acid, soluble	Humic Acid, insoluble Humin.

The brown humin substances are insoluble in water and alkalies, but are rendered soluble by fusing with caustic soda or potash, from the solution of which humic acid can

[23] In the light of recent investigations on the nature of organic matter of the soil it is necessary to revise this relict of the older terminology. The term "humus" is rather to be regarded as a loose generic term applicable to a group of organic compounds found in the soil.

again be precipitated. The humic acids comprise substances thrown down as brown collodial precipitates by mineral acids or alkaline extracts of humus. The humic acids (their chemical composition is insufficiently known), containing possibly 59 to 63 per cent C., 4.4 to 4.6 per cent H, and 35 to 36 per cent O, are easily dissolved in alkalies and reprecipitated from their solutions by stronger mineral acids. If they are withdrawn from acid soils or from ground decayed wood with alkalies or NH_3 and precipitated with HCl, a voluminous, gelatinous substance is obtained which, in drying, forms a brown or black amorphous mass. The humic acids are separated from their solution by freezing, in the form of a dark-colored powder, which gradually passes over again into solution.

Products similar to these are obtained in a large number of decompositions of the carbohydrates, both simple and complex. Trusov (1915) reports experiments in which it was found that the humification of various organic compounds consists of both chemical and biological processes, woody substances being humified by chemical compounds and fungi, albumin by biological processes alone, and substances containing tannin and chlorophyll by chemical processes alone. He found that the process of humification was aided by good aeration and relatively high temperatures. The time necessary for complete humification of the various compounds varied, albumin requiring a longer period than lignin substances containing tannic acid and chlorophyll. Starch was humified very slowly. Water extracts of undecomposed woody substances were very active in humus formation. Humus was not formed from proteids from substances containing tannic acid and chlorophyll, and was formed from lignin only when that substance decomposed together with albumin.

While it is true that the tendency in the decay of organic matter is toward simpler compounds and ultimately to a few simple compounds or the elements, the material known as soil organic matter is in the transition stage from the com-

plex compounds of living organisms to the simple ultimate products.

By the advancing decomposition, the nitrogen which in organic combinations is accessible to plants with difficulty, is carried over into compounds easily absorbed. In proportion as the carbohydrates are attacked by destructive agencies, the residue tends to constitute itself into a complex of increasing resistance. This entire group of by-products is extremely ill-defined and requires much more exhaustive investigation to establish their definite relationships with the carbohydrates from which they result. The partially decomposed material of woody plants forms a particularly vague and indefinite group of substances containing all the non-volatile products of fungal, enzymic and oxidative reactions on the plant residues. A detailed study of this group thus being out of question, we can merely ascertain what relation it bears to the original woody substance, since we have already discovered, in a general way, the particular constituents of the woody plant that entered into its formation.

The formation of the brown humic substance in woods decayed by *Polyporus pargamenus* is similar to the description given by von Schrenk (1900[1]) of that occurring in pecky cypress, except that none of the intermediate stages of the humification described by him could be detected. In the decay of dicotyledonous woods by *Polyporus pargamenus* the transformation of lignified membranes to humic substance is much greater and decidedly more abrupt than occurs in coniferous woods attacked by the same fungus. After comparing the description of the formation of the humic compound with that of the method of disintegration of the wood, it seems that the formation of humic compounds is due to certain chemical changes in the normal lignified membranes, as a result of which certain of its constituents which ordinarily react with phloroglucin-HCl, are extracted. These preliminary changes are followed by more profound changes ending in the formation of certain by-products of humic nature. These substances ordinarily diffuse through the adjoining cells, and ultimately harden within the lumina

of the woody elements surrounding them. Oftentimes all the remaining contents of the cells, including starch grains, fungal hyphæ that may have penetrated, etc., are covered with the same substance. From the manner of occurrence and distribution of the humic substance found in wood surrounding decayed areas of a trunk it would seem that this substance is formed as a by-product from the action of a fungus on the membranes of the woody substance, and that incidentally it is probably one of the products effective in preventing the unlimited spread and destructive action of the fungus.

MEANS OF ENTRANCE AND RATE OF DECAY.

The general occurrence of any given species of fungus over wide areas differing greatly in character, and the multitude of sporophores produced in any one locality, shows that spore formation and dissemination is of enormous magnitude. Every sporophore produces, figuratively speaking, "millions" of spores, and each perfectly formed spore carries with it the possibilities of the formation of a new plant, provided that spore falls on a suitable substratum and meets with conditions suitable for growth. For their dissemination the spores are dependent upon a great number of agencies, the most effective agency being wind which may carry these bodies for miles. Insects, especially the beetles, are also an aid in spore dissemination, since, after feeding on the sporophores, they escape bearing spores which they carry elsewhere. While innumerable spores are formed and disseminated — many chances thus being given for the development of new plants — the difficulty with which the spores germinate, owing to unfavorable natural conditions, is very great. Of the relatively small number of spores that actually succeed in falling on a suitable substratum and germinating thereon but few ever develop to mature plants owing to numerous adverse influences. Owing to the peculiar requirements of the spore for germination and further development, hundreds or thousands usually fail to develop where

a few find suitable conditions and give rise to mature plants. Moreover, spores are microscopically small and hence cannot contain very much nutriment. They cannot, therefore, withstand unfavorable conditions for germination for such protracted periods as can most seeds of seed-bearing plants. While spores frequently can pass through a long resting period and are capable of germination at the end of this period, after germination has begun the spore usually cannot resist unfavorable conditions. After a consideration of these facts it becomes apparent that the fungi in general must necessarily be very prodigal of their spores, so that they are produced in enormous numbers.

The relation of the fungus to its host is a definite one. The question of the spores gaining entrance, however, is somewhat problematic. But few of even the parasitic fungi can gain entrance unaided through the bark which envelops the entire living trunk, since the fungal hyphæ are incapable of forcing their way through layers of cork. When uninjured, the bark therefore serves as an efficient barrier to the entrance of even the parasitic fungi. For its entrance to the living tree *Polyporus pargamenus* is dependent upon human, organic, or inorganic agencies, usually gaining entrance through mechanical injuries to the host. There is no reason to believe that the fungus studied here can gain entrance to a living tree unaided by one of these methods of entrance, since the writer's experience has shown that there must be some condition conducive to infection, such as a broken branch or other form of wound, a drying out and consequent death of the cambium as a result of fire. When the cambium of a tree is killed and the underlying sapwood exposed by a broken branch, blazing, or some other form of mechanical injury, the wood immediately underlying the wounded area soon becomes functionless and dead. The weathering action of the elements softens this wood, it retains moisture readily, and affords an ideal environment for the development of a spore. The spores that are blown there by the wind germinate and send out their mycelial filaments, which slowly penetrate the dead wood. Some

plants, as the one studied here, seem to have acquired the ability to avail themselves of the parasitic habit, while during the greater part of their lives they are true saprophytes. In other words, at times in their development they may become parasitic, though nominally they are saprophytic.

Like many other fungi, *Polyporus pargamenus* possesses great adaptability, as shown by the fact that it attacks living tress as well as dead trees, stumps, and logs, thus showing that it may be either saprophytic or parasitic. Although it usually is found on dead wood, it may occur frequently on living trees where these have been severely wounded. This fungus is to be classed with the hemisaprophytes (the facultative parasites of DeBary). It is a plant that is wont to pass through its whole development as a saprophyte, its natural habitat being moist dead wood; under certain conditions, however, it may become a wound parasite.

The effect of such a parasite on the host may remain unnoticed for some time, since the growth of the mycelium is very slow at first and only a few wood cells are attacked. Upon becoming securely established within the tissues of the host, the mycelium spreads rapidly, permeating a larger volume of wood. After the mycelium penetrates the tissues of the host to a sufficient extent to be enabled to extract from them adequate nutrient materials for its sustenance, thereby causing what we call decay, it may produce fruiting bodies. The appearance of the fruit bodies often is the first noticeable indication of the presence of a fungous disease (Plate XXX.) The first appearance of the fruit-bodies on the bole of the infected tree, therefore, gives us an indication of the approximate development of the mycelium within the sapwood. As the vegetative part of the fungus increases in consequence of its age, so does the number of fruit-bodies increase. The dead portion of the sapwood is disintegrated slowly and, from contact with this, the adjoining living cells are reduced in vitality and ultimately die. When this stage is reached the effect on the host may be noticed in the dead branches at the top of the tree and the pale color of the remaining foliage. The fruit-bodies, like most annual ones,

grow very fast, and, after attaining maturity, they are destroyed by insect larvæ or they die and decay. During this time the mycelium of the fungus spreads rapidly, attacking hitherto sound sapwood, and in the following year new fruit-bodies are produced which give further indication of the spread of the mycelium throughout the wood, and, consequently, of the extent of the decay. After building up considerable strength in its saprophytic life the fungus proceeds to attack the growing zone of the trunk, that is, where the sapwood joins the bark and where the living substance is produced by very thin-walled cells. Thus the host is slowly killed and the fungus continues to live on in its saprophytic way. The remaining sapwood soon becomes changed to a brittle substance having none of the properties of wood. These changes soon kill the tree by girdling it and eventually weaken the trunk so that it is only a question of time until the tree becomes broken by the wind. At this stage the basal portion of the trunk, up to a height of several feet, usually is surrounded entirely by a luxuriant growth of fruit-bodies froming a closely imbricated mass (Plate XXXI, Fig. 1.)

Polyporus pargamenus is one of the wood-rotting fungi which commonly appear on standing deciduous trees after forest fires have killed a portion of the cambium. One cannot help but take cognizance of the total destruction caused by a large forest fire, but few even apprehend the extent of damage done by a small surface fire which quickly consumes whatever superficial litter there may be lying on the ground at the time. Such fires, although they may not seem to have injured the trees at the time, usually generate sufficient heat to kill the inner, living bark and cambium over a considerable area at the bases of the trunks. The bark over such areas dries out and cracks, causing the death of the underlying sapwood. It is in such dead areas that fungi find a ready entrance. The injury thus caused apparently is slight, but in reality the damage done may continue during the entire life of the tree and eventually cause its death. Such small fire scars are responsible for a large amount of fungous

decay and insect attacks in trees. The fire may have occurred many years ago and all signs of it been hidden by subsequent growth, but during the two or more years that it took the tree to heal over the scar insects and spores of fungi which produce rot in trees entered at this open wound on the butt and, in the case of the rots, have been at work ever since, gradually destroying the wood of the trunk (Plate XXXI, Fig. 2.) Thus it is that within a few months after the fire the sporophores *Polyporus pargamenus* are found growing on the dead bark and the decay caused by the fungus extends rapidly throughout the deadened area.

The small fire-scar may, and usually does, heal over so that within a few years no evidence of a fire or injury to the trunk can be seen from the outside. The rot, however, continues to grow for years, speedily causing the death of the tree upon the decay of the cambium and the sapwood. After the death of the tree the fungus continues its ravages of decay in the sound wood remaining, thus ruining the tree for most commercial purposes. Every time a tree is reached by a fire sufficiently hot to kill a small area of the inner bark and sapwood, an opportunity is given for attacks by this and other wood-destroying fungi.

There are, however, certain physical factors upon which the growth of fungi and the consequent destruction of the wood is dependent. For example, all fungi require a certain supply of nutriment, moisture, and air, the amount of each varying with the individual species and the environmental conditions for growth. If deprived of the requisite amounts of any one of these the fungus ceases to develop and eventually dies. It has been established that no chemical reaction takes place between substances except in the presence of water. As the decay of wood is largely dependent upon the chemical reaction of certain enzymes, secreted by the mycelium of the fungus, upon the various constituents of the cell-walls of the woody tissue, it follows that water must be present wherever there is decay. Water is essential for plant growth, and when there is no moisture no plants can develop, hence no decay can occur. Warmth also is conducive to the

growth of fungi, the most favorable temperature being about 90 degrees F. They cannot grow in extreme cold, although no degree of cold that occurs naturally will kill them after they have become well established.[24]

Like all sap-rotting fungi, *Polyporus pargamenus* is especially dependent for its development upon the presence of a sufficient quantity of water and air. It usually grows with the greatest vigor close to the surface of the soil. Its fruit-bodies may therefore be looked for at the base of trees and at or near the ground line on ties, posts, and all timbers exposed to the soil. Where wood has time to dry partially on the outside after it has been cut, the spores will not germinate owing to the lack of moisture. Infection of such partially dried wood usually takes place through some season check.

Polyporus pargamenus may start development in a stick of wood within a few weeks after it has been cut, or, in other words, shortly after the wood becomes sufficiently dried on the outside to form season checks. After it has once gained entrance below the surface the mycelium will grow vigorously in the wood and give absolutely no macroscopic evidence of its presence on the outside until the mycelium has become sufficiently developed to form fruit bodies, which then usually form by growing out through the season checks to the outside air. It is on account of its ability to produce decay in the interior of the wood that this fungus is so very destructive, and it is for this reason that the greatest care should be taken to guard against its possible entrance. In moist climates the fruiting bodies will form above the ground on moist wood which may be several feet above the ground. Where wood has a chance to have air circulate around it continuously, however, the possibilities of its becoming infected with this fungus are remote.

[24] Buller (1912) showed that the fruit bodies of *Schizophyllum commune* Fr., after having been kept dry and exposed to air for 2 years and 8 months, are able to retain their vitality when subsequently they have been dried in *vacuo* and subjected to the temperature of liquid air (— 190° C.) for three weeks. The retention of vitality was indicated by the fact that, upon being moistened, the fruit-bodies commenced to shed spores.

Polyporus pargamenus as a sap-rotting fungus is especially notorious for attacking those ties, timbers, and logs from which the bark has not been removed. The rapidity with which felled trees may be attacked and rotted by this fungus is a factor that must be taken into account when logging hardwoods, especially in the Southern Appalachian region. The destruction of the sapwood by this and other sap-rotting fungi often is so serious that unusual means often must be resorted to in order to get logs out of the woods before their value depreciates materially. Ordinarily the trees are attacked by a large number of sap-rotting fungi very shortly after they are felled, particularly if they are cut in the months from March to October. The rate of the destruction of the sapwood by these fungi varies greatly, however, according to the durability of the respective woods in question.

The decay which *Polyporus pargamenus* brings about in wood is usually confined for a year or more to the sapwood, and in many species it is largely confined to the sapwood. This is true of such trees that have their heartwood sharply differentiated from their sapwood as in the oaks. It is only after the sapwood is completely decayed that the heartwood is attacked to any great extent. Even then it is decayed far more slowly than the sapwood due to its greater durability. The manner and extent of the decay, of course, varies greatly not only with the species of tree, but also with the development of heartwood and its chemical and physical qualities. In the woods where the differentiation between the heartwood and sapwood is indistinct, as in the willows, poplars and birches, the fungus brings about the destruction of the sapwood with great rapidity and even destroys the heartwood with almost, if not equal, celerity. This variation is to be attributed to the greater durability possessed by the woods having a deep-colored heartwood and is due to the greater infiltrations of tannins, oils, and resins which render the wood more resistant to decay-producing fungi. The rate at which the sapwood of different dicotyledonous species decays presents little variation. The rate at which the heart-

wood decays, however, is proportional to the durability possessed by each species. It may be stated as a general rule that the sapwood of all trees is very susceptible to the attacks of *Polyporus pargamenus* and that where there is any difference in the resisting powers of such woods to this fungus it will be in favor of the heartwood.

A Reconnaissance Survey of a Recent Burn.

A reconnaissance survey was made in a region near State College, Pa., known locally as "The Barrens." This region was lumbered several years ago and since then parts of it have been burned over at frequent intervals by surface fires. It is characterized by having a dry, sandy soil, but the margin towards State College, where the survey was made, borders upon a limestone country, at which point the water is well underground except during the early months of the year.

In May, 1915, a surface fire swept over a portion of the Barrens that had thus far remained free from fire during the life of the stand of timber then present. As a result the trees on this area, with a few exceptions, were scorched so badly that they were killed outright. A few of the smaller trees were burned so badly near the base that some subsequently broke off. In August, 1916, the writer visited this area with the intention of securing some data relative to the rapidity with which fire-killed timber becomes infected with and deteriorates under the action of *Polyporus pargamenus*. In cruising through this area it was observed that a surprisingly large percentage of the fire-killed timber already (only one year and three months after the fire) bore sporophores of this sap-rotting fungus. Since the opportunity was so ably presented for securing valuable data in regard to the deterioration of standing timber after a forest fire, the writer decided to make a detailed reconnaissance survey of a portion of this burned area. A place was selected where the conditions were typical of the whole area that had been burned for the first time during the life of the stand and a rectangle, 100 by 500 feet, was laid off. This tract was fairly level — in fact no great variations in topographic conditions occur

within this area. All trees along the inside of the compass line were chalked to mark definitely the boundary of the tract. The following data was secured for each standing tree within this tract: species, diameter (measured to the nearest inch) at breast height, condition (as to whether dead or living), and the species of fungi growing upon it as evidenced by the sporophores upon the trunk. The principal trees on this tract were white oak (*Quercus alba* Linn.) and scarlet oak (*Quercus coccinea* Muenchh.), the former being by far the more abundant, although its average size was much smaller. Other species in the order of their abundance were white pine (*Pinus strobus* Linn.), mocker nut hickory [*Hicoria alba* (Linn.) Britton], red maple (*Acer rubrum* Linn.), chestnut [*Castanea dentata* (Marsh.) Borkh.], and pitch pine (*Pinus rigida* Mill.).[25] The data obtained is given below, the trees being tabulated by diameter under the species. The coniferous trees (37 white pines and 1 pitch pine) have been omitted from the summary since the fungus in question rarely grows on coniferous timber and these two species were not considered to be possible hosts for it.

[25] A single pitch pine, the sole survivor of the previous generation, was the only representative of this species.

A Reconnaissance of a Burn One Year and Three Months Old.

Species.	D. B. H. inches.	Fungi Present as Evidenced by the Sphorophores.			
		Polyporus pargamenus.	*Daldinia vernicosa.*	*Nummularia Bulliardi.*	*Hydnum ochraceum.*
Quercus alba[26]	2		*	*	
Quercus alba	2			*	
Quercus alba	2				
Quercus alba	2				
Quercus alba	2				
Quercus alba	2				
Quercus alba	2				
Quercus alba	2				
Quercus alba	2				
Quercus alba	2		*		
Quercus alba	2	*	*		
Quercus alba	2				
Quercus alba	3				
Quercus alba	3				
Quercus alba	3	*			
Quercus alba	3		*		
Quercus alba	3				
Quercus alba	3		*		
Quercus alba	3		*	*	
Quercus alba	3		*		
Quercus alba	3	*			
Quercus alba	3	*			
Quercus alba	3				
Quercus alba	3				*
Quercus alba	3	*	*		
Quercus alba	3	*			
Quercus alba	3				
Quercus alba	3	*			
Quercus alba	3	*			
Quercus alba	3	*	*		
Quercus alba	3	*			
Quercus alba	3		*		
Quercus alba	3				
Quercus alba	3		*		
Quercus alba	3				
Quercus alba	3				
Quercus alba	3	*			
Quercus alba	3	*			
Quercus alba	3	*			
Quercus alba	3	*			
Quercus alba	3	*			
Quercus alba	3	*			
Quercus alba	3	*			
Quercus alba	3				
Quercus alba	3				
Quercus alba	3				
Quercus alba	3				
Quercus alba	3				

[26] All trees not indicated by (L) after their diameters are dead.

A Reconnaissance of a Burn One Year and Three Months Old—(*Continued*).

Species.	D. B. H. inches.	Fungi Present as Evidenced by the Sphorophores.			
		Polyporus pargamenus.	*Daldinia vernicosa.*	*Nummularia Bulliardi.*	*Hydnum ochraceum.*
Quercus alba	3	.....	*	*	.....
Quercus alba	3	.....	*	.....	.....
Quercus alba	3	.....	.....	.....	.....
Quercus alba	3	.....	.....	.....	.....
Quercus alba	3	.....	.....	.....	.....
Quercus alba	3	.....	.....	.....	.....
Quercus alba	3	*	*	.....	.....
Quercus alba	3	*	*	.....	.....
Quercus alba	3	*	*	.....	.....
Quercus alba	3	*	.....	*	.....
Quercus alba	3	.....	.....	.....	.....
Quercus alba	3	.....	*	.....	.....
Quercus alba	3	.....	*	.....	.....
Quercus alba	3	.....	.....	*	.....
Quercus alba	4	*	*	.....	.....
Quercus alba	4	*	.....	*	.....
Quercus alba	4	.....	*	.....	.....
Quercus alba	4	.....	*	.....	*
Quercus alba	4	.....	.....	.....	.....
Quercus alba	4	.....	.....	.....	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	.....	.....	.....	*
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	*	*	.....	.....
Quercus alba	4	.....	.....	.....	*
Quercus alba	4	.....	.....	.....	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	.....	.....	.....	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	.....	.....	*	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	.....	.....	.....	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	.....	.....	*	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	.....	.....	.....	.....
Quercus alba	4	.....	.....	.....	.....
Quercus alba	4	.....	.....	.....	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	*	.....	.....	.....
Quercus alba	4	*	*	.....	.....
Quercus alba	4	.....	.....	.....	.....
Quercus alba	4	.....	.....	.....	.....
Quercus alba	5	*	.....	.....	.....
Quercus alba	5	*	*	.....	*
Quercus alba	5	.....	.....	.....	.....

A Reconnaissance of a Burn One Year and Three Months Old—(*Continued*).

Species.	D. B. H. inches.	Fungi Present as Evidenced by the Sphorophores.			
		Polyporus pargamenus.	*Daldinia vernicosa.*	*Nummularia Bulliardi.*	*Hydnum ochraceum.*
Quercus alba	5			*	
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*	*		
Quercus alba	5	*			
Quercus alba	5				
Quercus alba	5	*		*	
Quercus alba	5	*	*		
Quercus alba	5	*	*		
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*			
Quercus alba	5	*	*		
Quercus alba	5	*		*	
Quercus alba	5	*		*	
Quercus alba	5	*		*	
Quercus alba	5				
Quercus alba	6				*
Quercus alba	6				
Quercus alba	6	*	*		
Quercus alba	6	*	*		
Quercus alba	6	*	*		
Quercus alba	6				
Quercus alba	6	*			
Quercus alba	6	*			
Quercus alba	6	*			
Quercus alba	6	*			
Quercus alba	6	*			
Quercus alba	6	*			
Quercus alba	6	*			
Quercus alba	6	*			
Quercus alba	6	*			
Quercus alba	6	*	*		

A Reconnaissance of a Burn One Year and Three Months Old—(*Continued*).

Species.	D. B. H. inches.	Fungi Present as Evidenced by the Sphorophores.					
		Polyporus pargamenus.	*Daldinia vernicosa.*	*Nummularia Bulliardi.*	*Hydnum ochraceum.*	*Polyporus gilvus.*	*Schizophyllum commune.*
Quercus alba...	6	*	.....	.....	.....	.....	.....
Quercus alba...	6	*	.....	.....	.....	.....	.....
Quercus alba...	6	*	.....	.....	.....	.....	.....
Quercus alba...	6	*	.....	.....	.....	.....	*
Quercus alba...	6	.....	.....	*	.....	.....	.....
Quercus alba...	6	*	.....	.....	.....	.....	.....
Quercus alba...	6	*	.....	.....	.....	.....	.....
Quercus alba...	6	*	.....	.....	.....	.....	.....
Quercus alba...	6	*	.....	.....	.....	.....	.....
Quercus alba...	6	*	.....	.....	.....	.....	.....
Quercus alba...	6	*	.....	.....	.....	.....	.....
Quercus alba...	6	.....	.....	.....	.....	.....	.....
Quercus alba...	6	*	.....	.....	.....	.....	.....
Quercus alba...	6	*	.....	.....	.....	.....	.....
Quercus alba...	6	.....	.....	.....	.....	.....	.....
Quercus alba...	6	*	*	.....	*	.....	.....
Quercus alba...	6	*	*	.....	.....	.....	.....
Quercus alba...	7 (L)	.....	.....	.....	.....	.....	.....
Quercus alba...	7	.....	.....	*	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	*	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	*	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	7	.....	.....	*	.....	.....	.....
Quercus alba...	7	*	.....	.....	.....	.....	.....
Quercus alba...	8	*	.....	.....	.....	.....	.....
Quercus alba...	8	*	.....	.....	.....	.....	.....
Quercus alba...	8	*	.....	.....	.....	.....	.....
Quercus alba...	8	*	.....	.....	.....	.....	.....
Quercus alba...	8	*	.....	.....	.....	.....	.....
Quercus alba...	8	*	.....	.....	.....	.....	.....
Quercus alba...	8	*	.....	.....	.....	.....	.....
Quercus alba...	8	*	.....	.....	.....	.....	.....
Quercus alba...	8	*	.....	.....	.....	.....	.....

A Reconnaissance of a Burn One Year and Three Months Old—(*Continued*).

Specifs.	D. B. H. inches.	Fungi Present as Evidenced by the Sporophores.				
		Polyporus pargamenus.	*Daldinia vernicosa.*	*Nummularia Bulliardi.*	*Hydnum ochraceum.*	*Polyporus tulipiferus.*
Quercus alba...	8	*	.....	.....	.....	*
Quercus alba...	8	*	.....	.....	.....	.....
Quercus alba...	8	.....	.....	.....	*	.....
Quercus alba...	8	*	.....	.....	.....	.....
Quercus alba...	8	.....	.....	.....	.....	.....
Quercus alba...	8	*	.....	.....	.....	.....
Quercus alba...	8	*	.....	.....	.....	.....
Quercus alba...	8	*	.....	.....	.....	.....
Quercus alba...	8	*	.....	.....	.....	.....
Quercus alba...	9	*	.....	*	.....	.....
Quercus alba...	9	*	.....	.....	.....	.....
Quercus alba...	9	*	.....	.....	.....	.....
Quercus alba...	9	*	.....	.....	.....	.....
Quercus alba...	9	*	.....	.....	.....	.....
Quercus alba...	9	*	.....	.....	.....	.....
Quercus alba...	9	*	.....	.....	.....	.....
Quercus alba...	9	*	.....	*	.....	.....
Quercus alba...	10	*	.....	.....	.....	.....
Quercus alba...	10	*	.....	.....	.....	.....
Quercus alba...	10	*	.....	.....	.....	.....
Quercus alba...	11	*	.....	.....	.....	.....
Quercus alba...	11	*	.....	.....	.....	.....
Quercus alba...	11	*	.....	.....	.....	.....
Quercus alba...	11	*	.....	.....	.....	.....
Quercus alba...	11	*	.....	.....	.....	.....
Total.....	237	164	.....	.....	.....	.....

A Reconnaissance of a Burn One Year and Three Months Old—(*Continued*).

Species.	D. B. H. inches.	Fungi Present as Evidenced by the Sporophores.			
		Polyporus pargamenus.	*Daldinia vernicosa.*	*Nummularia Bulliardi.*	*Hydnum ochraceum.*
Quercus coccinea	5				
Quercus coccinea	5	*			
Quercus coccinea	6				
Quercus coccinea	6				
Quercus coccinea	7	*		*	
Quercus coccinea	7				
Quercus coccinea	7				
Quercus coccinea	7	*			
Quercus coccinea	7				
Quercus coccinea	7	*			
Quercus coccinea	8	*			
Quercus coccinea	8				
Quercus coccinea	8				
Quercus coccinea	8				
Quercus coccinea	8				*
Quercus coccinea	8				
Quercus coccinea	8	*			
Quercus coccinea	9		*		
Quercus coccinea	9				
Quercus coccinea	9				
Quercus coccinea	9				
Quercus coccinea	9				
Quercus coccinea	9	*			
Quercus coccinea	10				
Quercus coccinea	10	*			
Quercus coccinea	10	*			
Quercus coccinea	10			*	
Quercus coccinea	10 (L)				
Quercus coccinea	10				
Quercus coccinea	10				*
Quercus coccinea	10	*			
Quercus coccinea	10	*			
Quercus coccinea	10				
Quercus coccinea	10				
Quercus coccinea	10			*	
Quercus coccinea	10			*	
Quercus coccinea	10				
Quercus coccinea	10				
Quercus coccinea	10	*		*	
Quercus coccinea	11	*			
Quercus coccinea	11	*			
Quercus coccinea	11				
Quercus coccinea	11				
Quercus coccinea	11			*	
Quercus coccinea	11	*			
Quercus coccinea	11				
Quercus coccinea	11	*		*	
Quercus coccinea	11	*			
Quercus coccinea	12	*			
Quercus coccinea	12	*			
Quercus coccinea	12				
Quercus coccinea	12				
Quercus coccinea	12	*			
Quercus coccinea	12				
Quercus coccinea	12				

A Reconnaissance of a Burn One Year and Three Months Old—(*Continued*).

Species.	D. B. H. inches.	Fungi Present as Evidenced by the Sporophores.			
		Polyporous pargamenus.	*Daldinia vernicosa.*	*Nummularia Bulliardi.*	*Hydnum ochraceum.*
Quercus coccinea	12				
Quercus coccinea	12				
Quercus coccinea	12				
Quercus coccinea	12	*			
Quercus coccinea	12	*			
Quercus coccinea	13				
Quercus coccinea	13 (L)	*			
Quercus coccinea	13	*		*	
Quercus coccinea	13	*			
Quercus coccinea	14	*			
Quercus coccinea	14	*		*	
Quercus coccinea	14 (L)	*			
Quercus coccinea	15				
Quercus coccinea	15	*			
Quercus coccinea	16 (L)				
Quercus coccinea	18	*			
Total	71	30			

A Reconnaissance of a Burn One Year and Three Months Old—(*Continued*).

Species.	D. B. H. inches.	Fungi Present as Evidenced by the Sporophores				
		Polyporus pargamenus.	*Daldinia vernicosa.*	*Hypnum orchraceum.*	*Schizophyllum commune.*	*Polyporus ulipiferus.*
Hicoria alba	1		*			
Hicoria alba	1					
Hicoria alba	1		*			
Hicoria alba	1					
Hicoria alba	1					
Hicoria alba	1					
Hicoria alba	1					
Hicoria alba	2					
Hicoria alba	2					
Hicoria alba	2					
Hicoria alba	2					
Hicoria alba	2		*			
Hicoria alba	2		*			
Hicoria alba	2					
Hicoria alba	2					
Hicoria alba	2			*	*	
Hicoria alba	2		*			
Hicoria alba	2		*			
Hicoria alba	2					*
Hicoria alba	3					
Hicoria alba	3		*			
Hicoria alba	3	*				
Hicoria alba	3	*	*		*	
Hicoria alba	3					
Hicoria alba	3	*				
Hicoria alba	4					
Hicoria alba	4					
Hicoria alba	4					
Hicoria alba	4					
Hicoria alba	4					
Hicoria alba	5					
Hicoria alba	5				*	
Hicoria alba	5					
Hicoria alba	6					
Hicoria alba	7		*			
Total	35	3				
Acer rubrum	1					
Acer rubrum	1					
Acer rubrum	1					
Acer rubrum	3	*				
Acer rubrum	3	*				
Acer rubrum	5	*				
Acer rubrum	5	*				
Acer rubrum	5	*				
Acer rubrum	5	*				
Acer rubrum	5	*				
Acer rubrum	6	*				
Acer rubrum	6	*				
Acer rubrum	7	*				
Acer rubrum	7	*				
Acer rubrum	11					
Total	15	11				

A Reconnaissance of a Burn One Year and Three Months Old—(*Concluded*).

Species.	D. B. H. inches.	Fungi Present as Evidenced by the Sporophores.		
		Polyporus pargamenus.	*Polyporus abietinus.*	*Polyporus volvatus.*
Castanea dentata	1			
Castanea dentata	1			
Castanea dentata	1			
Castanea dentata	2	*		
Castanea dentata	5			
Castanea dentata	12			
Total	6	1		
Pinus strobus	1		*	
Pinus strobus	1			
Pinus strobus	2			
Pinus strobus	2			
Pinus strobus	3			
Pinus strobus	3			
Pinus strobus	3			
Pinus strobus	3			
Pinus strobus	4			
Pinus strobus	4			
Pinus strobus	4			
Pinus strobus	4			
Pinus strobus	5			
Pinus strobus	5			
Pinus strobus	5			
Pinus strobus	5			
Pinus strobus	5			
Pinus strobus	5			
Pinus strobus	5			
Pinus strobus	6			
Pinus strobus	6			
Pinus strobus	6			
Pinus strobus	6			
Pinus strobus	6			
Pinus strobus	6			
Pinus strobus	7			
Pinus strobus	7			
Pinus strobus	8			
Pinus strobus	8			
Pinus strobus	8			
Pinus strobus	8			
Pinus strobus	9			
Pinus strobus	10			
Pinus strobus	11			
Pinus strobus	11			
Pinus strobus	11 (L)			
Pinus strobus	12			
Total	37	0		
Pinus rigida	9			*
Total	1	0		

Summary of Trees Bearing Sporophores of Polyporus Pargamenus by Species and Size.

Species.	D. B. H. inches.	Number of trees on area.	Number bearing sporophores of *P. pargamenus.*	Percentage bearing sporophores of *P. pargamenus.*
Quercus alba	2	12	1	8
Quercus alba	3	52	21	40
Quercus alba	4	37	21	57
Quercus alba	5	40	36	90
Quercus alba	6	33	27	82
Quercus alba	7	27	24	89
Quercus alba	8	19	17	89
Quercus alba	9	8	8	100
Quercus alba	10	3	3	100
Quercus alba	11	6	6	100
Total *Quercus alba*	.....	237	164	69
Quercus coccinea	5	2	1	50
Quercus coccinea	6	2	0	0
Quercus coccinea	7	6	3	50
Quercus coccinea	8	7	2	29
Quercus coccinea	9	6	1	17
Quercus coccinea	10	16	5	31
Quercus coccinea	11	9	5	56
Quercus coccinea	12	12	5	42
Quercus coccinea	13	4	3	75
Quercus coccinea	14	3	3	100
Quercus coccinea	15	2	1	50
Quercus coccinea	16	1	0	0
Quercus coccinea	18	1	1	100
Total *Quercus coccinea*	.....	71	30	42
Hicoria alba	1	7	0	0
Hicoria alba	2	12	0	0
Hicoria alba	3	6	3	50
Hicoria alba	4	5	0	0
Hicoria alba	5	3	0	0
Hicoria alba	6	1	0	0
Hicoria alba	7	1	0	0
Total *Hicoria alba*	.....	35	3	9
Acer rubrum	1	3	0	0
Acer rubrum	3	2	2	100
Acer rubrum	5	5	5	100
Acer rubrum	6	2	2	100
Acer rubrum	7	2	2	100
Acer rubrum	11	1	0	0
Total *Acer rubrum*	.....	15	11	73
Castanea dentata	1	3	0	0
Castanea dentata	2	1	1	100
Castanea dentata	5	1	0	0
Castanea dentata	12	1	0	0
Total *Castanea dentata*	.....	6	1	17
Total all species of hard-woods	.....	364	209	57

The figures given above are striking indeed and show that *Polyporus pargamenus*, as judged by the frequency of its occurrence, is the only wood-destroying fungus to be reckoned with as yet in this particular locality. The rapidity of the infection and growth of this pernicious sap-rotting fungus is remarkably well demonstrated by the fact that, out of the total (364) standing hardwood trees upon this tract, 57 per cent bore sporophores of *Polyporus pargamenus* within one year and three months after the area had been burned (Plate XXX). Here it may be mentioned that the weather was very dry during the two months prior to the survey so that practically all the growth of the fungus may be credited to thirteen months. Of the trees bearing no sporophores of the fungus a few were charred so badly near the ground that the chances for infection were materially reduced, owing to the fact that little or no sapwood was left near the ground, a place which offers the optimum moisture conditions for the growth of wood-destroying fungi. Moreover, many of the trees which do not yet bear sporophores are undoubtedly infected by this sap-rot so that, before many more months elapse, a much higher percentage of the trees will bear sporophores. In addition new trees are constantly becoming infected. The white oak is the principal tree on this tract, and, of the 237 white oak trees recorded, 69 per cent bore sporophores of *Polyporus pargamenus*. It is especially interesting to note that the smaller the trees were the less was the percentage containing sporophores of this sap-rot. Of the two-inch trees only 8 per cent bore sporophores, while of the three-inch trees 40 per cent bore sporophores. From this point on as the diameters of the trees increased so did the percentage that bore sporophores, until 100 per cent was obtained for the nine, ten and eleven-inch trees which were the largest present upon this particular tract. No apparent relations between the diameter of the trees and the percentage bearing sporophores were evident in the other species but there were more white oak trees on the tract than of all the other species combined, so that for this species better and more uniform comparisons are to be expected.

The majority of the fire-killed trees had sent up a good coppice growth but even this new growth will be subjected constantly to infection and as soon as any injuries occur to any of these new trees they will, without fail, be attacked by this sap-rotting fungus. The majority of the standing timber on this tract is too small to serve for anything but fence posts and cordwood, but even the possibility of profitable returns from these sources has been neglected by the owner. Thus will the infected timber remain standing for a number of years and continue to be a place of propagation and source of new infections, thereby endangering all other hardwood timber for miles around.

Control of the Sap-rot Caused by Polyporus Pargamenus

In forest pathology we have to deal with trees under two cultural types: First, the trees in the forest; second, shade, park, and ornamental trees. When we come to consider the question of commercial control, which is the principal aim and end of forest pathology, we can see that we have two very different lines of attack, which are governed entirely by commercial considerations. A shade or ornamental tree has great individual value and is under constant observation, or at least it should be. In this case we can employ in the prevention of disease the methods of control that have been evolved with such remarkable success in tree surgery practice.

When we consider diseases of the forest, however, commercial conditions are quite different. It is no longer possible to give the individual tree a large amount of attention. We must consider the forest *en masse*. This being the case, it is apparent that there is indicated for forest pathology a line of evolution quite distinct from that which characterizes the application of forest pathology in arboricultural practice. For the present this development will be comparable to what a physician would term "preventive medicine," as in the case of animal or human disease when we consider the species *en masse*. In the protection of forests the control of wood-destroying fungi therefore must be a matter of prevention

rather than one of cure. In the control of such diseases as the sap-rots we have recourse only to slight modifications of silvicultural practice which will enable such diseased trees to be marked for removal when the forest is cut. There is one forest operation in which a timbered tract may be easily cleared of diseased stems at small cost. This is the repeated process of thinnings or of making improvement cuttings, during which all diseased and backward trees should be removed. In forests of high value, with high-priced timber located near towns or centers of industry, this cleaning out is comparatively easy and the value of the products sold usually suffices to pay for the improvement cutting. In remote forests, however, with a small working staff, deficient means of transportation, and little or no market for the thinned-out material, such methods are impracticable.

The sap-rot caused by *Polyporus pargamenus* is one of the most important sap-rots of deciduous trees. Suggestions made for its control will apply more or less to all of them. So long as fires are allowed to run through our woodlots and forests of deciduous trees, sap-rots will continue to be common. The loss of good, merchantable timber in lumbering operations due to wood-destroying fungi that have followed forest fires is enormous. Long (1913), in a study of the "Effect of Forest Fires on Standing Hardwood Timber," made in the Ozark Mountains of Arkansas, cites a case where on one stave sale area seventy-six trees out of every 100 felled had butt rot and twenty-seven trees in every 100 had wormholes of some kind in them. As the author states, this means that after going to the expense of felling 100 trees only twenty-four of them were perfectly sound and suitable for staves; not only was there a monetary loss from the cull of seventy-six trees, but the expense of felling unsound trees must be considered. For five widely separated areas in the eastern part of this forest Long states that an average of sixty-five trees in every 100 had butt rot and twenty-six had wormholes sufficient to cull some of the bolts. Most of this loss could be traced directly to the fires so common in this forest. The area where seventy-six trees in every 100 were

found to have butt rot has been burned over regularly for years. Over areas where fires had not been so frequent the injury from butt rot was correspondingly less.

We find, then, that forest fires are a serious menace to hardwood timber since they open the way not only to wood-destroying fungi but also to wood-boring insects. Every fire, therefore, only increases the damage by providing conditions for a new crop of insects in the trees and giving another chance for fungi to enter through the new fire scars, thus increasing the quantity of unmerchantable timber and decreasing the amount of money received for the timber. This deterioration in the standing timber of any region is the direct source of a tremendous loss to the entire community of that region, for, as Long (*l. c.*) states, the timber itself is not only a total loss to the settlers and other owners, but by its presence it also increases the cost of lumbering and decreases the stumpage value of that timber which is merchantable; furthermore, it means a loss in wages to the laborer and a loss to the State in revenues from the sale of government timber.

The fact follows, then, that the continued burning of timbered lands in any region of the country is causing an annual loss of thousands of dollars — an absolute detriment to the welfare of the states involved. It is obvious that this loss can be almost entirely eliminated by the prevention of all forest fires, whether large or small — a matter which can be accomplished only by the hearty co-operation of all the residents with the fire protection work of the individual states or the government.

The practice of leaving standing all the badly diseased trees in our woodlots and of leaving them remain uncut in a lumbered area is radically wrong from the standpoint of proper forest sanitation, for this practice enables sap-rotting fungi to maintain themselves in the forest while the new generation of trees slowly develops and as soon as any become injured they thus become susceptible to the attacks of sap-rotting fungi. Trees effected with sap-rot should not be left for seed trees wherever it is possible to leave healthy ones

for this purpose, since, having their vitality considerably reduced, they would not be good seed-producers, and moreover they undoubtedly would die within two or three years or even earlier. In deciduous forests it usually is unnecessary to leave seed trees, owing to the abundant production of sprouts and to the presence of young trees intermingled with the more mature ones.

Trees in the woodlot should be inspected annually and all diseased trees should be removed. The presence on a trunk of the fruiting bodies of *Polyporus pargamenus*, which may appear as early as a year from the time of infection, is the surest evidence of the existence of sap-rot and of the necessity of removing the tree. Such trees should be removed wherever found. Fire-scorched trees should be removed and marketed before decay sets in, for once the cambium is killed, decay invariably will follow quickly. In large forested areas it is not possible to personally inspect the trees every year, although the present prices of white oak nearly justify the expense necessary in a system of careful forest sanitation. It certainly will pay in lumbering large tracts of oak and other valuable hardwoods to cut out all unsound or diseased trees, remove the parts that can be used and burn the remainder. Under the present methods of lumbering many trees are left standing because they are decayed near the base of the trunk. The importance of utilizing such trees can not be too strongly exemplified, since, if used before the decay has spread for many months, the heartwood and all of the tree above the first log can be used, especially in those trees which have a durable heartwood, such as the white oak, for example. If cut down these trees will often be found to contain enough lumber to pay for the cost of the operation. Such a procedure will lead to a better and closer utilization of our gradually decreasing lumber supply of deciduous woods, especially of white oak. If, however, trees affected by sap-rot are left long in the forest they will deteriorate very rapidly and unless the merchantable timber which such trees may contain is utilized it will be a total waste and remain in the woods to furnish a means for the incubation of the fungus and the spread of the inoculum.

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Summary

Polyporus pargamenus is one of the most common wood-destroying fungi causing a sap-rot of most of the species of dicotyledonous trees occurring throughout its nearly cosmopolitan range. It is essentially a saprophytic organism, and as such is especially notorious for attacking dead wood, especially felled wood from which the bark has not been removed. It frequently becomes a wound-parasite, and as such is especially prevalent on fire-scarred trees throughout the hardwood forests of the eastern half of the United States.

The sporophores of *Polyporus pargamenus* are subject to wide variation in their morphological characters, and the various diverse forms are to be regarded as ecological adaptations of the fructification in response to varied environmental factors, particularly the moisture content of the substratum and the humidity of the air.

As a species *Polyporus pargamenus* consists of a number of more or less intergrading forms which often become sufficiently distinct as to constitute varietal forms or subspecies. It is advocated that these varietal forms be recognized for

practical purposes, particularly for the convenience of the critical worker.

The usual form of the fructification is distinct from that of its near relative *Polyporus abietinus,* with which it is often confused. These two species are to be distinguished definitely only by the combined use of their respective morphological characters, since the knowledge of the habitat (whether on coniferous or dicotyledonous wood), while sufficient in most cases, will not always serve as the deciding criterion.

The concentric sulcations, as well as the zones of color and pubescence, on the pilei are to be regarded as expressive of differences in the local climatological and atmospheric conditions existing at different times during the growth of the pilei.

The pores of the sporophores are evolved successively from the center of growth or point of attachment outward, the basidia and spores beginning to form while the pilei are still young, and continuing their development throughout the life of the pilei. As a result of this successive development of the basidia the spores are shed intermittently over long periods.

The extreme drouth resistance of the fructifications is indicated by the following criteria: (a) By the ability of the sporophores to resume growth after withstanding long periods of dessication; (b) by the ability of the sporophores to revive and shed viable spores after being kept in a state of dessication for at least a year; and (c) by the ability of the spores to germinate and produce infectious mycelium after having been shed and kept in a state of total dessication for as long as ten months.

Darkness is conducive to the most vigorous vegetative growth but retards sporophore formation. The dimidiate form of the sporophore is not to be ascribed either solely to the stimulus afforded by light, nor to that by gravity, but to the combined action of both. The formation of pores and the production of spores, however, depends entirely on light. No chemotropism of the mycelium could be detected; it seems

to be non-specialized and secures its nutrient substances from the easiest available source.

Germination of the basidiospores occurs regularly in a great number of nutrient media, but the percentage of germination and subsequent growth of the mycelium is directly proportional to the suitability of the culture medium used. Germination also occurs in both tap and distilled water, thus showing that an external food supply is not necessary for the germination of the spores, although it greatly accelerates it. Germination was not stimulated, but was greatly retarded, by the use of slight quantities of alcohol and ether. In their germination the spores exhibited no especial preference for either acid or alkaline nutrient media.

The change in the mycelium from the short-lived primary mycelium, which is the product of the elongating germ tubes, to the typical secondary mycelium apparently is a regular occurrence not influenced by the nature of the culture medium or by other external factors.

The occurrence of two secondary spore forms, namely oidia and chlamydospores, as definite stages in the life cycle of this plant is here reported for the first time. Oidia were observed to form repeatedly on both primary and secondary mycelium; chlamydospores, however, were observed to form only on the secondary mycelium. The formation of oidia apparently can continue indefinitely or at least for several successive generations.

The basidiosporic hymenium has been developed from the basidiospore in petri dish cultures on nutrient agar, and also from the mycelium contained in a bit of birch bark when inoculated on sterile blocks of wood, thus completing the life-cycle of this fungus.

The decay of wood by *Polyporus pargamenus* consists of a series of chemical and physical changes brought about by the reduction of the woody substance by enzyme secretions of the vegetative mycelium. The dissolution of the cell-walls is to be attributed to the fact that they, as a potential source of food, are valueless to the fungus until broken down and reduced to a condition suitable for translocation and assimilation.

The enzymatic digestion and consequent decay of wood by *Polyporus pargamenus* is accomplished mainly by the exceedingly minute fungal hyphæ, which are the ultimate branches of the mycelial system. Upon the completion of the decay within any given area of the wood the older mycelium, which has fulfilled its purpose, causes to function in the enzymatic reduction of the woody substance, although it still may prove useful in the translocation of the elaborated food materials. When the final stage of the decay is reached the mycelium itself apparently is dissolved together with the woody substance in areas of the wood where the decay is most intense.

The decay of wood by *Polyporus pargamenus* is characterized by its habitual tendency to produce a minute pocket type of decay, which, while not very pronounced in the early stages of the decay, becomes a conspicuous feature of the later stages. As a result of the intensity of the decay in these innumerable pockets the destruction of the woody elements becomes completed in these initial centers of the decay before the wood lying between these areas is materially destroyed. Within the individual pockets the decay progresses mainly in a direction parallel to that of the woody elements, the central elements becoming reduced rapidly to pith-like consistency. In the late stages two or more adjoining pockets may coalesce into one, the resulting pockets becoming quite empty of contents and separated by almost membranous layers of less decayed wood. The largest pockets observed were in yellow birch wood, where they attained a maximum diameter of three mm. in diameter and three cm. in length.

The first chemical change brought about by the action of this fungus is that of delignification. The decay begins at the interior of the cell-wall and destroys it progressively from the internal or last-formed layer to the middle or primary lamella between two adjoining cells, first removing the lignin constituents and then the remaining cellulose. The tertiary and secondary layers are entirely dissolved before the delignification of the middle lamellæ commences.

The results obtained from the study of the decay by *Polyporus pargamenus* establish the fact that the minor variations

in the decay of different woods by this fungus are much more dependent upon the dissimilar structure of the respective woods than has been generally supposed.

The results of the microscopic study of the decay of five woods of diverse structure, of the macroscopic study of the decay in twenty-eight other species of wood, indicate that the decay progresses to varying extents in different woods before reaching completion and that the decay of any given species approaches completion long before the woody substance is entirely destroyed. The ratio between the amounts of chemically resistant by-products accumulated in the woody tissue and the potential food supply still remaining available for assimilation by the fungus automatically constitutes itself an index of the completion of the decay.

The anatomical and microchemical observations on the decays of the five woods studied indicate that the vegetative mycelium of *Polyporus pargamenus* secretes diastatic, proteolytic, and cytohydrolytic enzymes, among the latter being pectinase, cellulase, and ligninase.

The metabolic by-products most frequently encountered in wood decayed by *Polyporus pargamenus* are the extremely chemically resistant brown humic products which infiltrate portions of the wood, causing them to appear as brownish discolored areas, or which more often collect in narrow zones between the decayed and undecayed portions, causing the wood at this point to appear as a blackish zone of varying thickness. These zones are not constant in position since they keep pace with the advance of the decay in any part of the stem and ultimately disappear upon its completion within that part.

The partially decomposed material of woody plants forms a particularly vague and indefinite group of substances containing all the non-volatile products of fungal, enzymic, and oxidative actions on the plant residues. The physical appearance and chemical composition of the brown humic by-products of decomposition vary greatly according to the extent to which they have been reduced. The chief characteristic of this series of degradation products of plant tissues is

the accumulation of carbon at the expense of oxygen and hydrogen. The cell contents and certain other substances, particularly the hemicellulose xylan (wood gum), that originally were combined with the cellulose to constitute the cell-wall, furnish the formative material which coagulates to thick drops and gives rise to the humic by-products of decomposition which ultimately infiltrate certain portions of the wood, causing them to appear as blackish zones.

By the action of a strong oxidizing reagent on fresh sap-wood a brown humic product can be prepared artificially, which is essentially like that occurring naturally in wounded areas of living trees, dead wood, or as the result of their decay by *Polyporus pargamenus* and other wood-destroying fungi.

The properties of the extracts obtained respectively from sound and decayed hickory wood indicate that in the course of the decomposition a portion of the carbohydrate substance, particularly the hemicellulose xylan, becomes converted into humic substances of two principal groups, namely humic acid and humin. It is the accumulation of these humic substances which give rise to the dark brown decomposition products which are of such common occurrence in decaying wood.

The chemically resistant by-products often forming blackish zones in wood decayed by *Polyporus pargamenus* have proven to be a group of substances analogous to the humic products which arise under certain circumstances in wounded parts of living trees or in fallen woody parts that may be entirely free from fungous attack and which have been known under the name "wound gum." In wood free from fungous attack the formation of the brown decomposition product is mainly dependent upon the concurrence of three factors: (a) The presence of dead cells; (b) an optimum supply of moisture; and (c) a supply of oxygen sufficient to promote oxidation. The formation of the brown product in this case is likewise a sign of the humification which sets in gradually when their walls and contents undergo decomposition.

In general the manner and extent of the decay varies greatly, not only with the species of tree, but also with the development of the heartwood and its chemical and physical

qualities. The rate at which the sapwood of various dicotyledonous species decays presents but little variation; the rate at which the heartwood decays, however, is slower by reason of being proportional to the superior durability of the heartwood over the sapwood exhibited by each species.

For its entrance to the living tree, *Polyporus pargamenus* is dependent upon human, organic, or inorganic agencies, usually gaining entrance through mechanical injuries to the host. Ordinarily this organism exists as a saprophyte but may, when favorable conditions present themselves, become a wound parasite. In the latter case it exhibits in its life-cycle two rather distinct phases — pathogenesis and saprogenesis.

The practice of allowing fires to run through our hardwood forests can not be too strongly condemned, since even trees but slightly scorched on one side furnish admirable infection courts for the entrance of *Polyporus pargamenus* and other sap-rotting fungi. The subsequent deterioration of the standing timber of any region incident to fire is a direct source of loss to the entire community of that region.

In a study of fire-killed timber made one year and three months after the burning, out of 364 standing hardwood trees occurring on an area 100 by 500 feet in central Pennsylvania, 57 per cent already bore sporophores of *Polyporus pargamenus*. Of the 237 white oak trees recorded, this being the principal tree on the tract, 69 per cent bore sporophores, the largest diameter classes containing the largest proportion of sporophore-bearing trees. This indicates the importance of the fungus in causing timber deterioration.

Under the conditions on this area the incubation period of *Polyporus pargamenus* was less than fifteen months, and, in all probability more nearly twelve months. In the case of artificial cultures the length of the entire life-cycle varied from four months in agar plate cultures to eighteen months in cultures on blocks of wood.

In the protection of our forests the control of *Polyporus pargamenus*, as well as other sap-rotting fungi, must be a matter of prevention rather than one of cure. Prevention

involves forest sanitation as carried out in such slight modifications of silvicultural practice as will enable diseased trees to be marked for removal when the forest is thinned out or cut. Such procedure, in addition to improving the woodlot, will lead to a better utilization of our gradually waning lumber supply of deciduous woods, particularly of white oak.

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PLATE I.

Sporophores of *Polyporus pargamenus*, showing upper and lower surface views, one-half natural size.

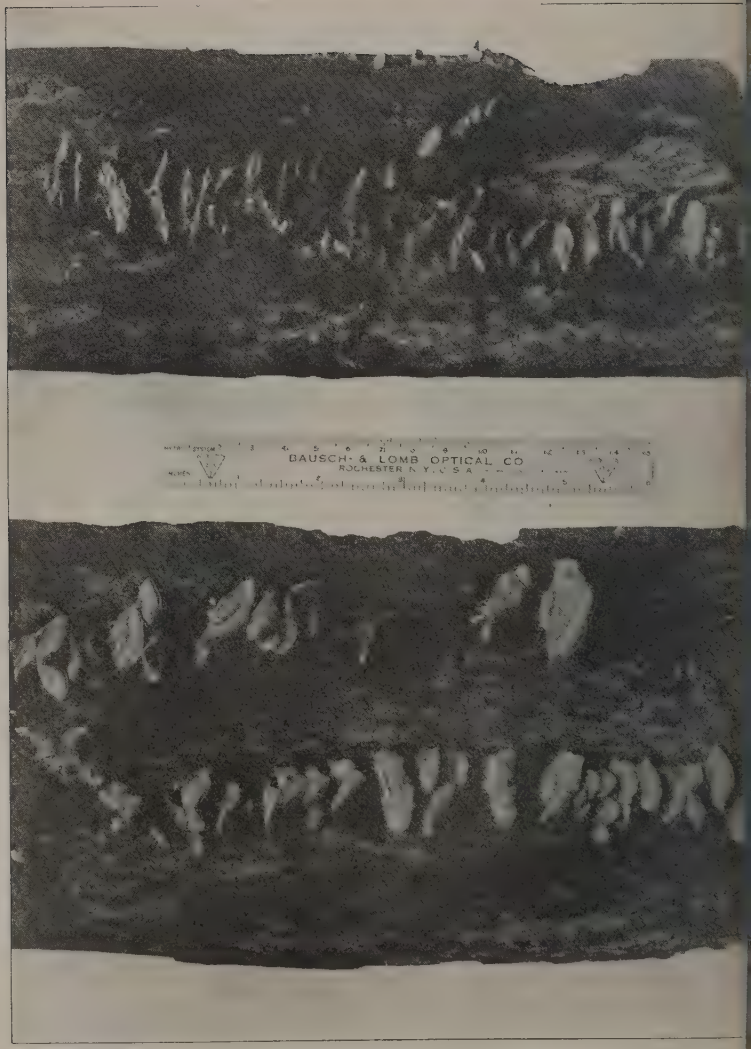


PLATE II.

Sporophores of *Polyporus pargamenus* (below) and *Polyporus abietinus* (abo
growing close together on a dead hemlock (*Tsuga canadensis*) trunk.

PLATE III.

Sporophores of *Polyporus pargamenus* on dead hemlock (*Tsuga canadensis*) trunk.

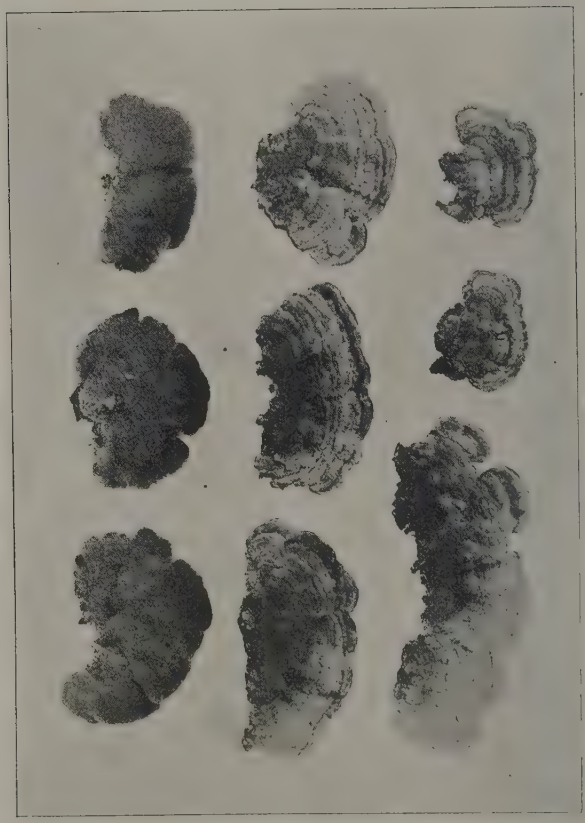


PLATE IV.

Sporophores of *Polyporus abietinus* on a dead hemlock (*Tsuga canadensis*) trunk, two-thirds natural size.

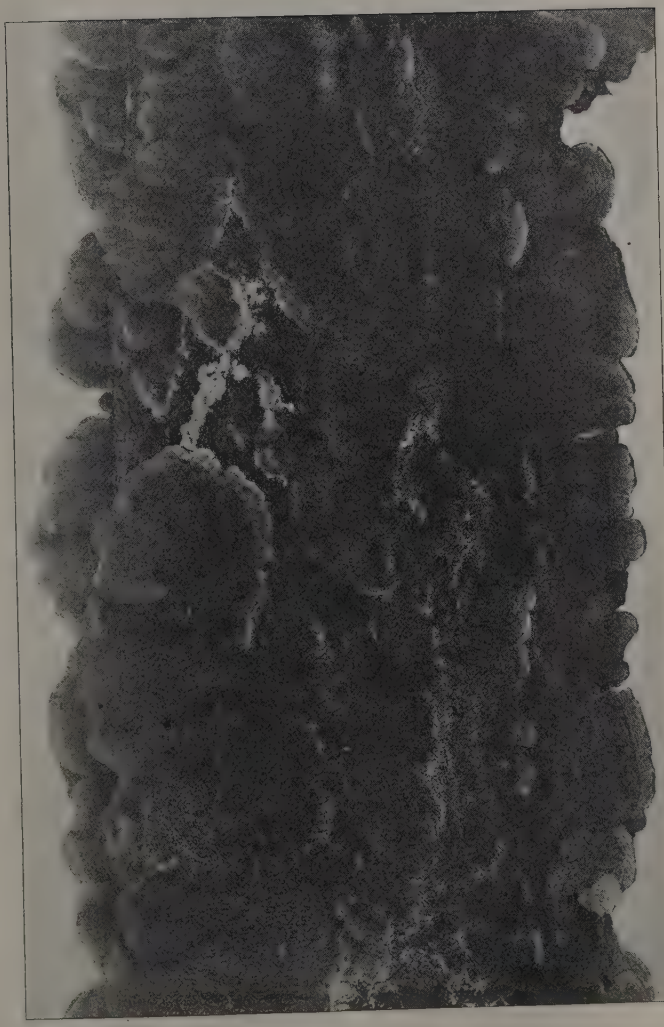


PLATE V.

Resupinate sporophores of *Polyporus pargamenus* growing on the under surface of a fallen branch of chestnut oak (*Quercus prinus*), two-thirds natural size.

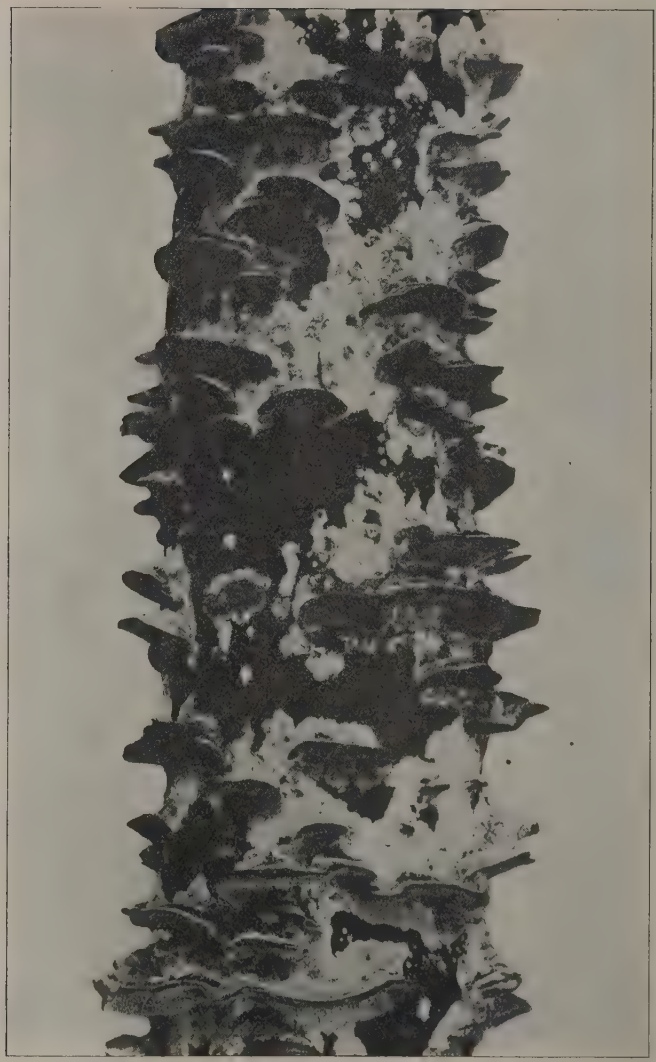


PLATE VI.

Poroid form of *Polyporus pargamenus* on a dead sapling of large-tooth aspen (*Populus grandidentata*), natural size. These sporophores had revived and the pilei exhibited two distinct layers of pores.

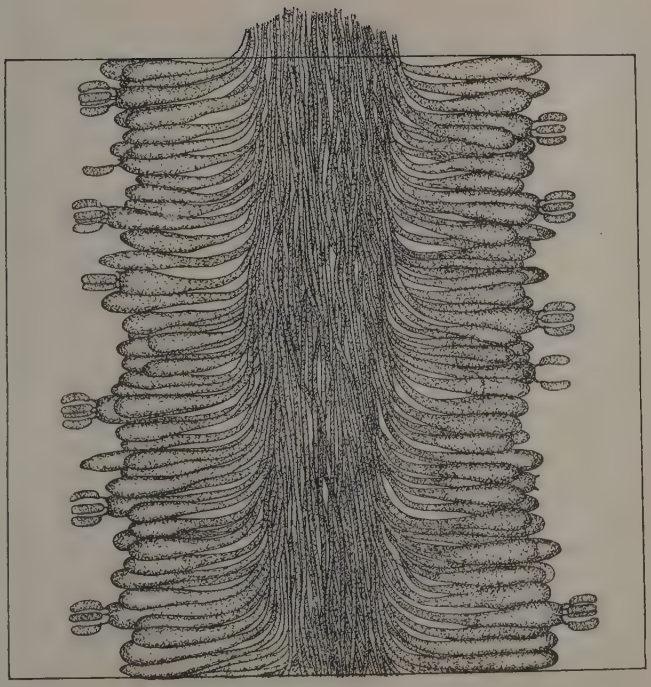


PLATE VII.

Camera lucida drawing of a section through hymenium of *Polyporus pargamenus*, showing the hymenial elements — the basidia and paraphyses — and the trama of the pores, X 1250. No cystidia were found in the sections cut of this sporophore.

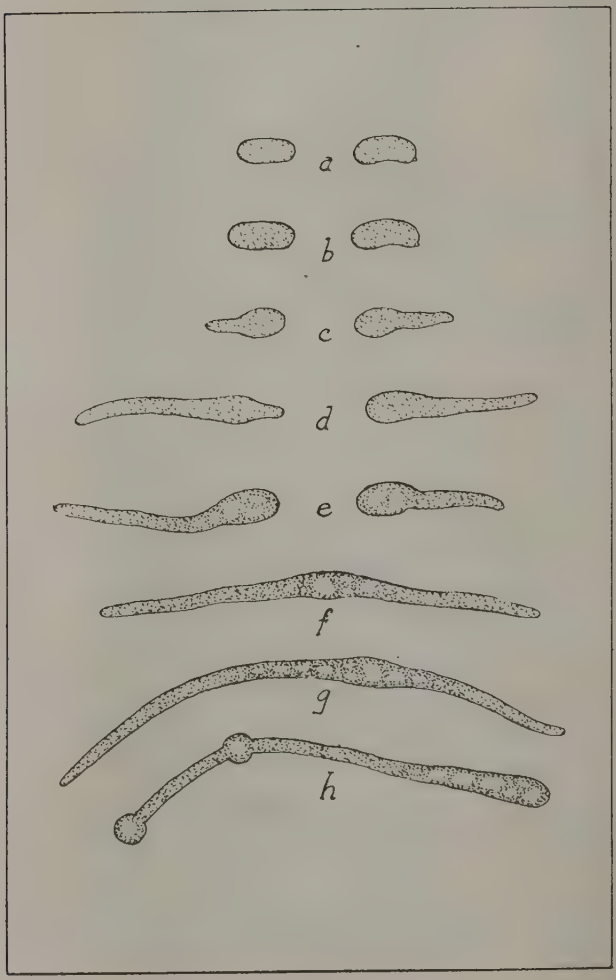


PLATE VIII.

Camera lucida drawing of germinated spores of *Polyporus pargamenus*, X 2000. *a*, spores at time of shedding; *b*, spores after remaining in hanging drop culture for 16 hours; *c*, spores from hanging drop culture after 20 hours; *d*, spores after 24 hours; *e*, spores after 28 hours; *f*, spore after 32 hours; *g*, spore after 36 hours; *h*, spore after 40 hours, showing two cysts.

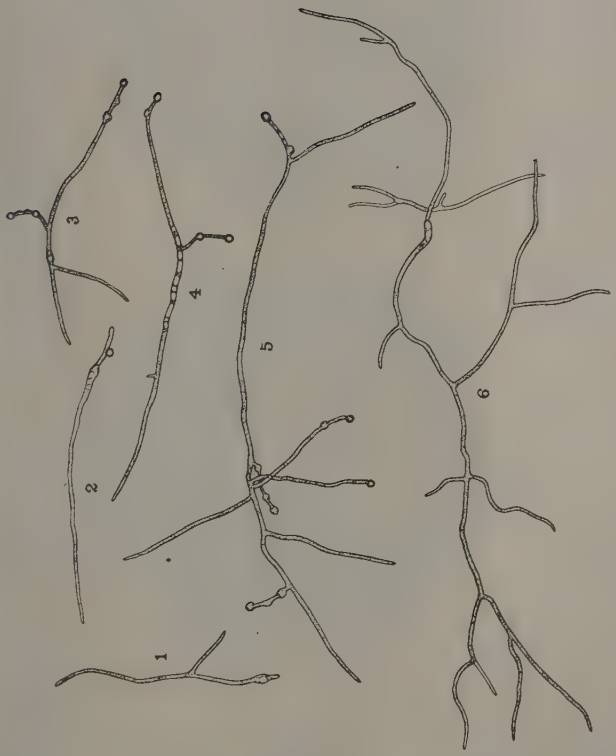


PLATE IX.

Camera lucida drawings of germinated spores of *Polyporus pargamenus*, X 500. *1* and *2*, spores from hanging drop culture after 2 days; *3*, spores after 3 days; *4*, spores after 4 days; *5* and *6*, spores after 1 week. Figures *2*, *3*, *4* and *5* show mycelium with cysts.

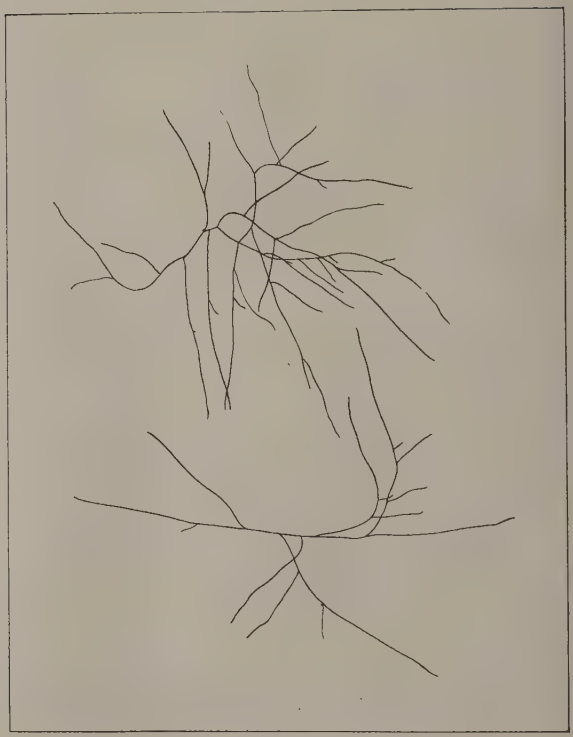


PLATE X.

Camera lucida drawings of the mycelium from two spores of *Polyporus pargamenus* grown in a 0.5% solution of sodium chloride, X 175.

Fig. 1.

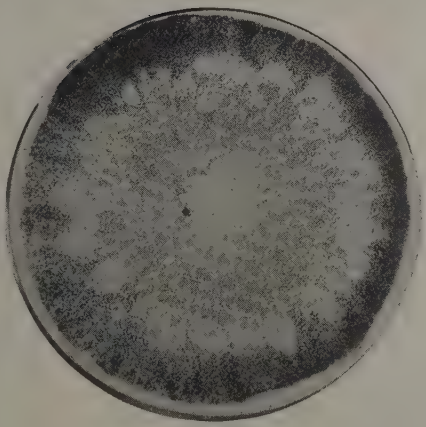


Fig. 2.

PLATE XI.

Fig. 1.— Mycelial growth on prune agar 1 month after the center of the plate was inoculated with basidiospores, two-thirds natural size. The mycelium arising from the basidiospores was the typical filamentous mycelium, possessing cross-walls and clamp connections, and exhibiting no tendency to break up into oidia.

Fig. 2.— Mycelial growth on malt agar extract 1 month after the center of the plate was inoculated with germinated oidia transferred from a hanging drop culture, two-thirds natural size. The mycelium arising from the oidia broke up into oidia constantly until it reached the side of the dish, after which it grew up off the agar and no longer formed oidia.

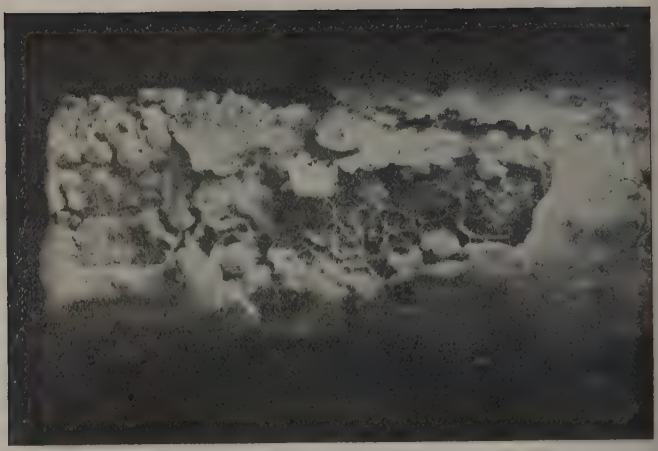


Fig. 1.

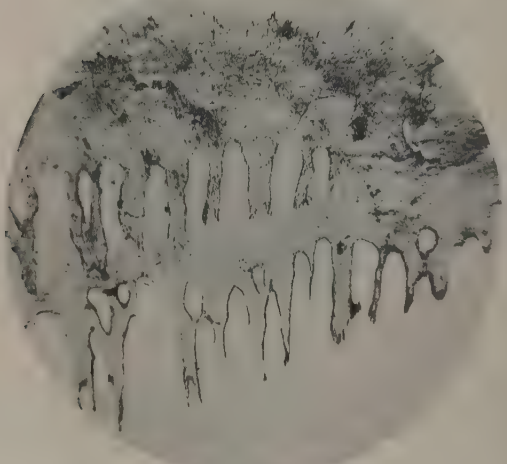


Fig. 2.

PLATE XII.

Fig. 1. Block of yellow birch (*Betula lutea*) wood inoculated in a large test tube by placing beside it a piece of decayed yellow birch wood containing active mycelium of *Polyporus pargamenus*.

Fig. 2. Photomicrograph of a longitudinal section of one of the revived sporophores shown in Plate 6, showing the two distinct layers of tubes. X 15.

PLATE XIII.

A culture of *Polyporus pargamenus* on blocks of fresh yellow birch (*Betula lutea*) wood secured by dropping into the flask with the sterilized blocks two or three small pieces of the inner bark of a yellow birch trunk containing active mycelium.

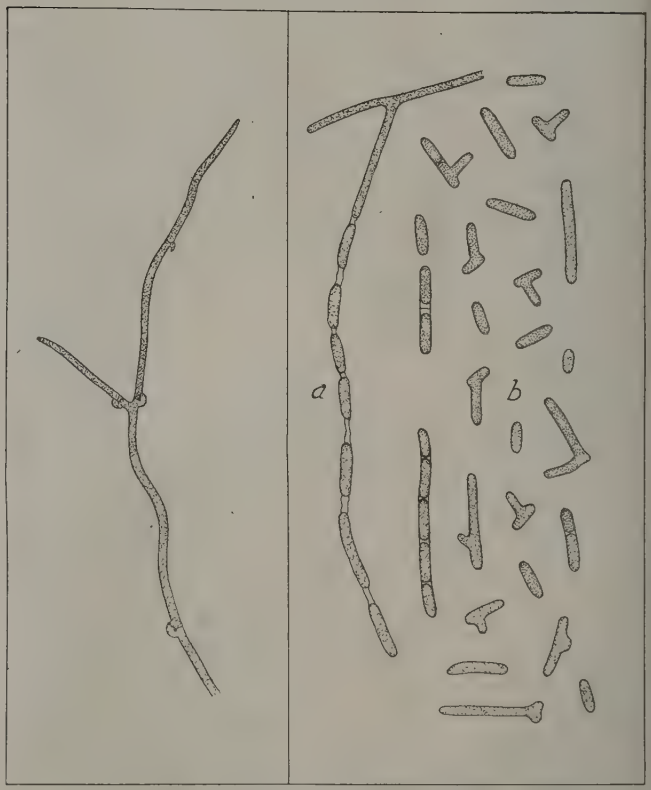


Fig. 1. Fig. 2.

PLATE XIV.

Fig. 1.— Portion of secondary hypha from hanging drop culture showing the clamp connections arising as lateral outgrowths of one cell and fusing with the cell beneath it, X 1,000.

Fig. 2.— Mycelium of *Polyporus pargamenus* breaking up into oidia, X 1,000. *a*, appearance of a hypha preliminary to the separation of the oidia. This hyphal filament was mounted dry on a glass slide and shows the collapse of the vacuolate portions of the hyphal membrane. When such hyphæ are mounted in water the vacuolate membranes quickly become turgid. *b*, a group of oidia showing the great diversity of their shape and size.

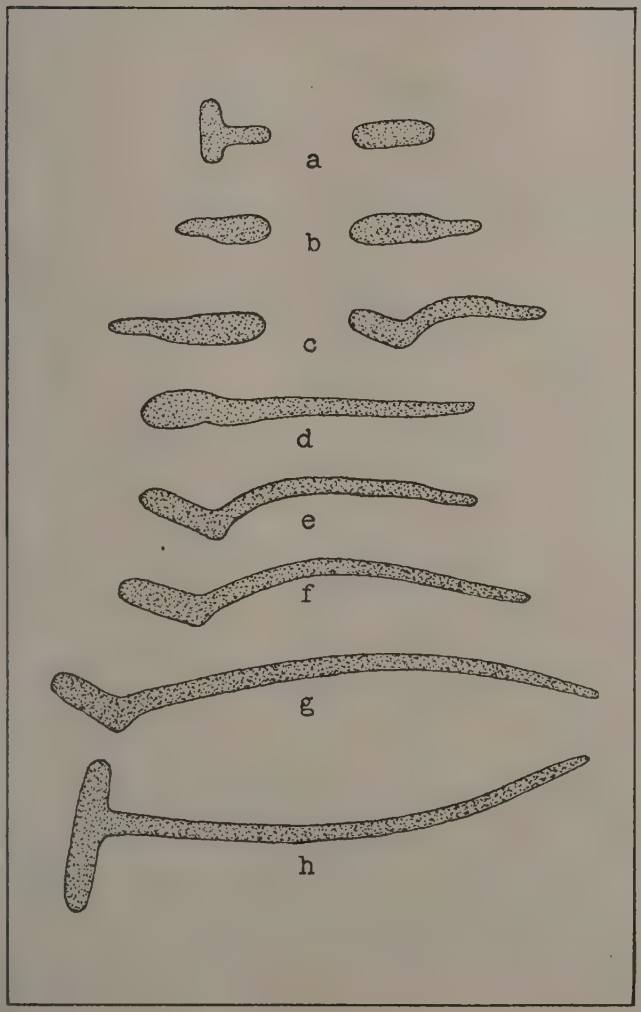


PLATE XV.

Camera lucida drawings of germinated oidia of *Polyporus pargamenus*, X 2,000. *a*, two oidia after they were set free from the parent hypha; *b*, oidia after remaining in hanging drop culture for 18 hours; *c*, oidia after 22 hours; *d* and *e*, oidia after 28 hours; *f*, oidium after 32 hours; *g*, oidium after 36 hours; *h*, oidium after 40 hours.

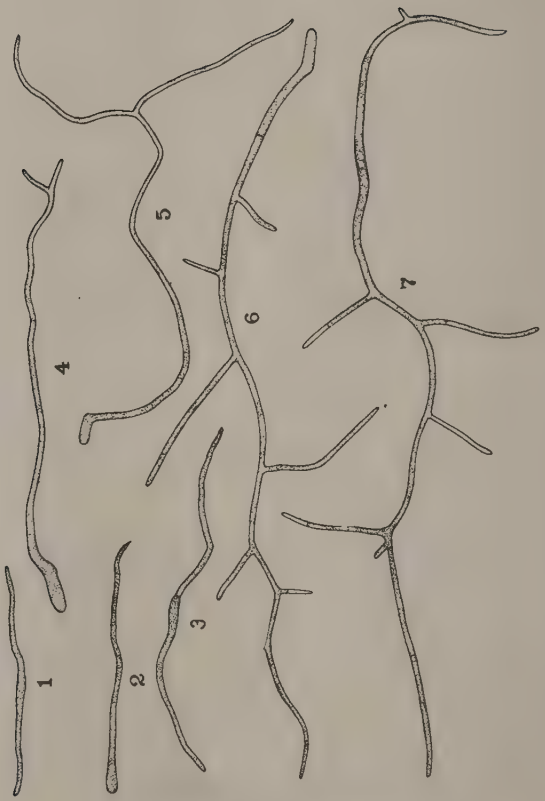


PLATE XVI.

Camera lucida drawings of germinated oidia of *Polyporus pargamenus* showing the formation of the primary type of mycelium, X 650. *1* and *2*, oidia from hanging drop culture after 2 days; *3*, oidium after 3 days; *4*, oidium after 4 days; *5*, oidium after 5 days; *6*, oidium after 6 days; *7*, oidium after 7 days.

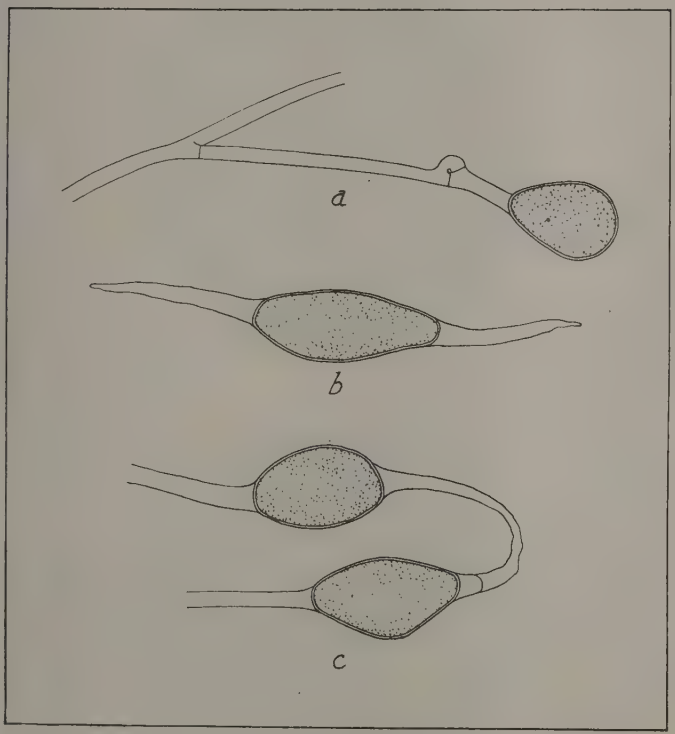


PLATE XVII.

Camera lucida drawings showing chlamydospore formation in old mycelium after it had passed through the oidial stage, X 1,500. *a*, a terminal chlamydospore; *b*, an intercalary chlamydospore, showing how it is set free by the disintegration of the empty portion of the parent hypha; *c*, two intercalary chlamydospores formed near together, showing the disintegration of the parent hypha. The lower chlamydospore has abandoned its original end wall, the protoplasm having contracted further and formed a new limiting membrane about itself at this point.

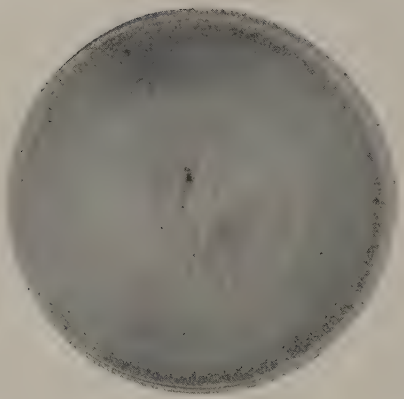


Fig. 1.

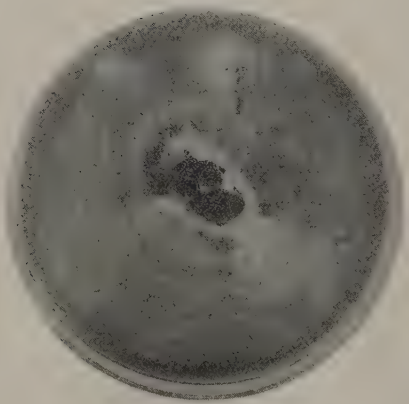


Fig. 2.

PLATE XVIII.

Fig. 1.— A 3-week's old culture of *Polyporus pargamenus* secured by transferring oidia from a culture on malt extract agar to a new plate of the same medium, two-thirds natural size. The mycelial growth resulting was indistinctly zonate and again broke up into oidia.

Fig. 2.— A 3-week's old culture of *Polyporus pargamenus* on malt extract agar secured by transferring to a plate a portion of the agar containing yellowish mycelium from an old oidial growth. The mycelial tissue transferred quickly developed into a brownish hydnoid hymenium while an oidial growth spread over the agar from this nearly to the side of the dish.

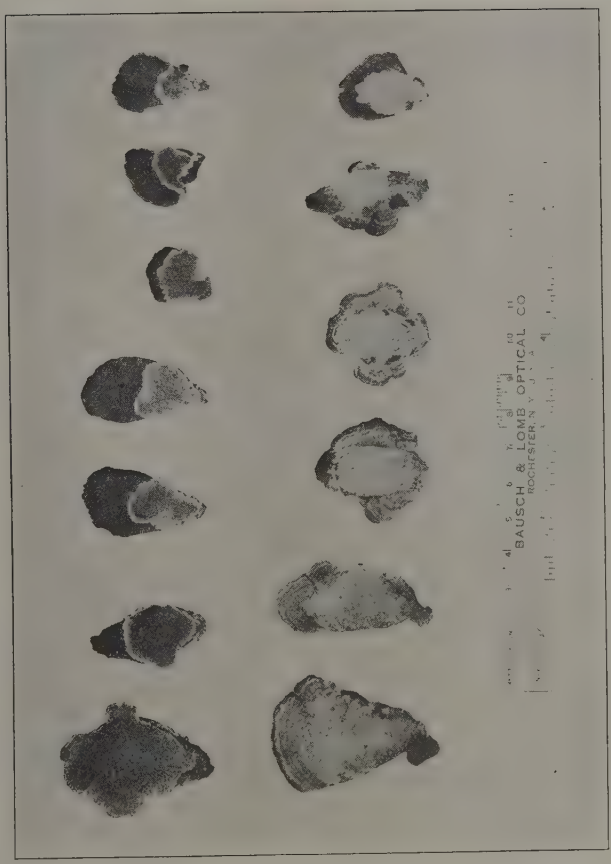


PLATE XIX.

A group of sporophores of *Polyporus pargamenus* that have revived and made a new growth the second year. The sporophores in the left hand row show the formation of a new hymenial layer over the old one, which, in the sporophore at the bottom of the row, has not only entirely obliterated the old sporophore but has grown out beyond the margin of it, thus increasing the size of the pileus. The sporophores in the right hand row show the formation of a new mold-like growth over the upper surface of the sporophores and the marginal additions to the old pilei resulting from the new growth.

PLATE XX.

Wood of *Betula lutea* decayed by *Polyporus pergamenus*, showing initial stages in the formation of pockets — tangential surface — natural size.

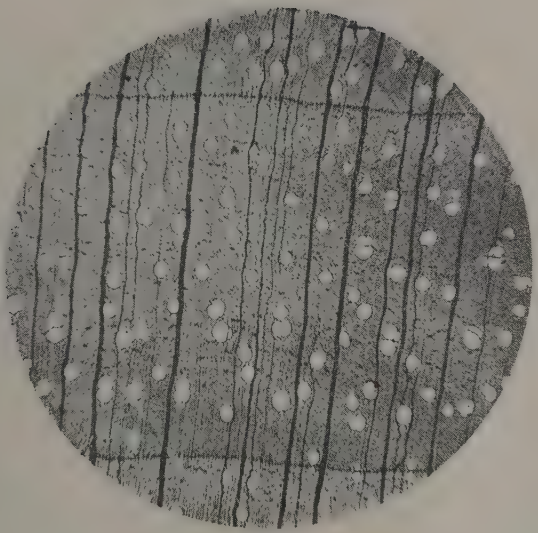


Fig. 1.

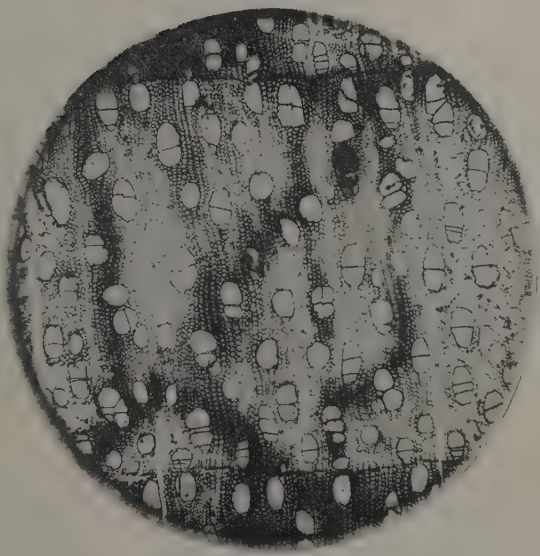


Fig. 2.

PLATE XXI.

Fig. 1.— Photomicrograph of a transverse section of normal yellow birch (*Betula lutea*) wood, X 20.

Fig. 2.— Photomicrograph of a transverse section of yellow birch (*Betula lutea*) wood decayed by *Polyporus pargamenus*, X 35.

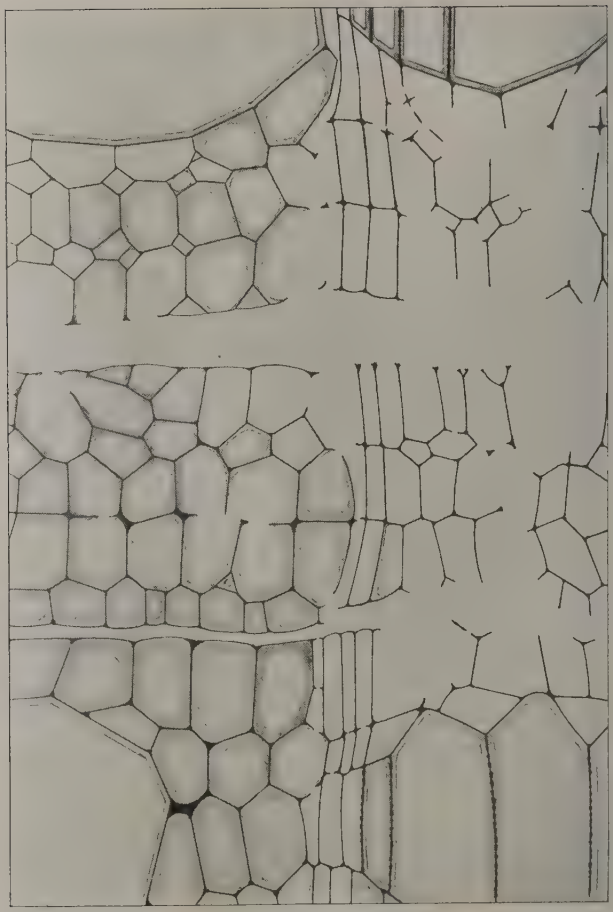


PLATE XXII.

Camera lucida drawing of transverse section of wood of yellow birch (*Betula lutea*) wood decayed by *Polyporus pargamenus*, X 800. The section, which was taken through two adjoining growth rings, shows the late wood on the left side and the early wood on the right side, with a group of vessels in each corner, and two pith-rays running horizontally through the center. The cells of the lower pith-ray have been completely dissolved out while the adjoining prosenchyma elements of the summer wood remain unaffected. The layers of secondary thickening of the elements in the early wood have been completely dissolved out, leaving only the middle lamellæ, a condition which gives the wood a skeletonized appearance.

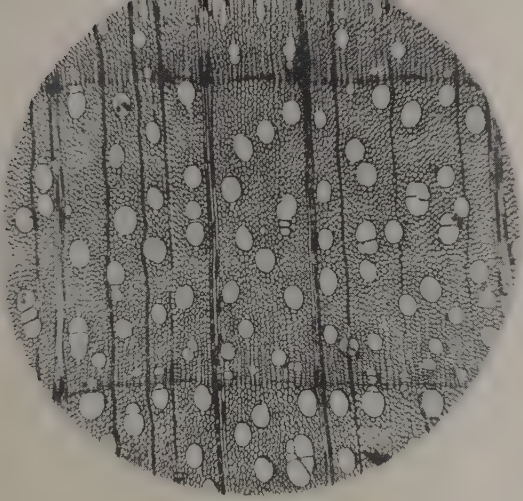


Fig. 1.

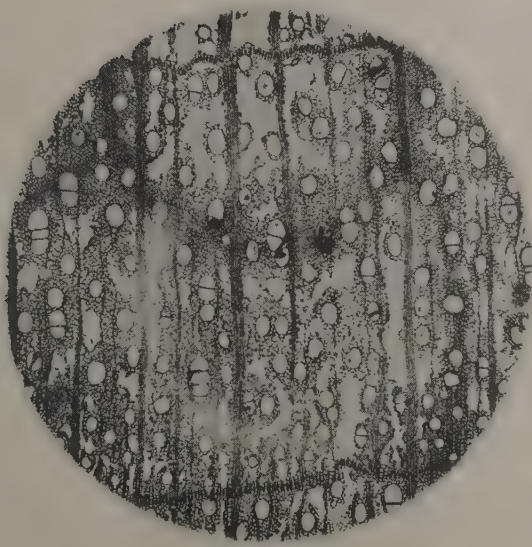


Fig. 2.

PLATE XXIII.

Fig. 1.— Photomicrograph of a transverse section of normal sugar maple (*Acer saccharum*) wood, X 40.

Fig. 2.— Photomicrograph of a transverse section of sugar maple (*Acer saccharum*) wood decayed by *Polyporus pargamenus*, showing the early dissolution of all the elements lying within the terminal cells of the growth ring save the multiseriate pith-rays and the vessels, X 35.

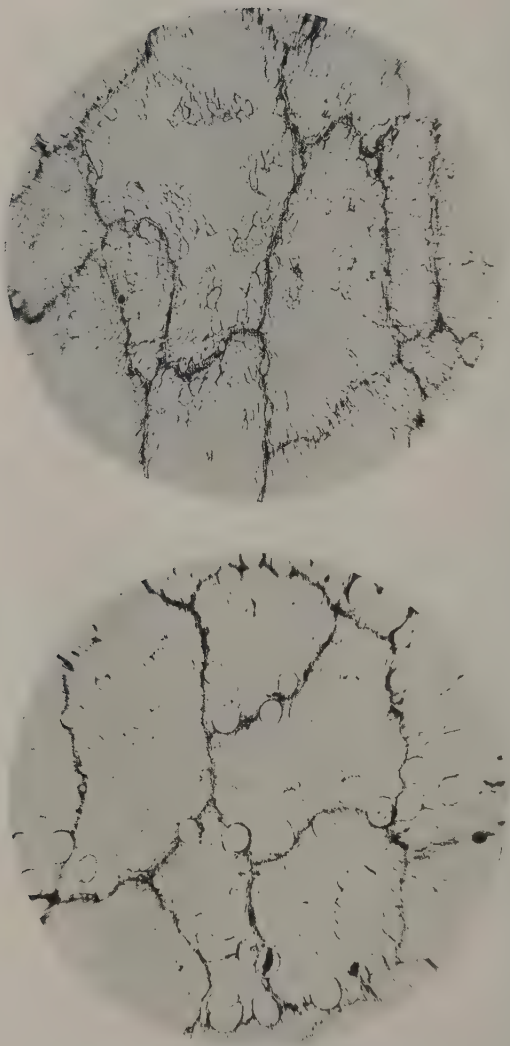


PLATE XXIV.

Fig. 1.— Photomicrograph of a transverse section of yellow birch (*Betula lutea*) wood showing the final stage of the decay, X 15.

Fig. 2.— Photomicrograph of a transverse section of bitternut hickory (*Hicoria minima*) wood showing the final stage of the decay, X 15.

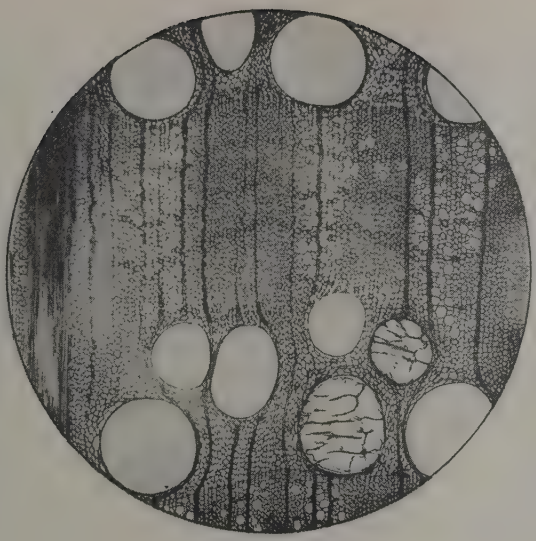


Fig. 1.

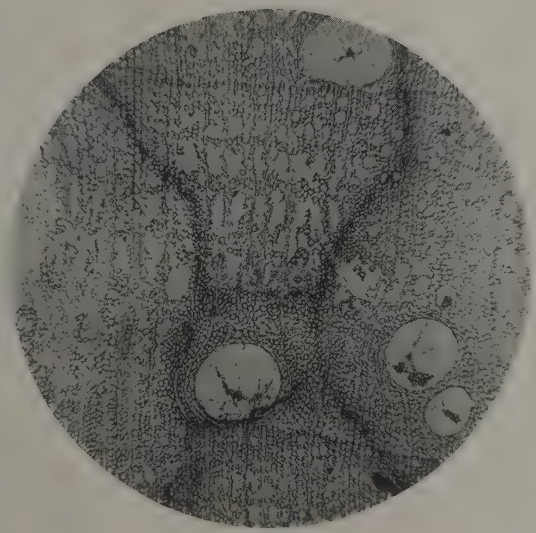


Fig. 2.

PLATE XXV.

Fig. 1.— Photomicrograph of a transverse section of normal chestnut oak (*Quercus prinus*) wood, X 35.

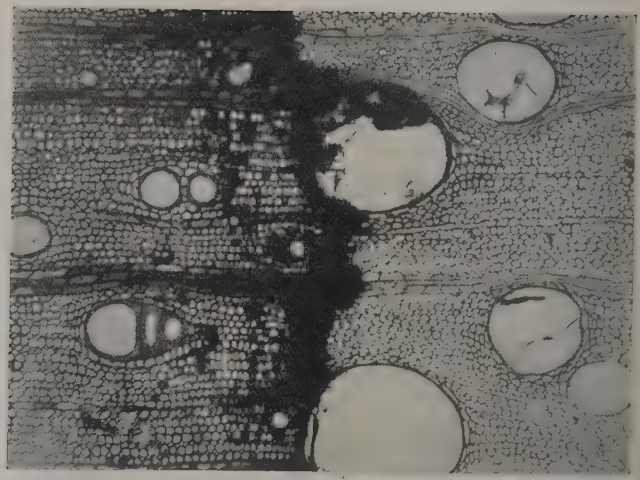
Fig. 2.— Photomicrograph of a transverse section of chestnut oak (*Quercus prinus*) wood decayed by *Polyporus pargamenus*, showing a reticulum of matted hyphæ bounding the original pockets or decayed areas, X 30.

PLATE XXVI.

Wood of hemlock (*Tsuga canadensis*) decayed by *Polyporus pargamenus*, showing the peculiar localization of the decay into small pockets — tangential surface – natural size. This shows the characteristic appearance of the wood in the late stages of decay.

PLATE XXVII.

The last portion of the sapwood of a pignut hickory (*Hicoria glabra*) log to decomposed by the action of *Polyporus pargamenus*, the remainder of the pwood having been completely decayed. The completely disintegrated wood thering to these comparatively sound pieces was removed by rubbing and scrapg. Note the black color of the superficial portions of these pieces of undecayed od. It was caused by the infiltration of abundant decomposition products into ose portions immediately adjoining the completely decayed wood. The central ce (marked X) shows one of these pieces in transverse section.



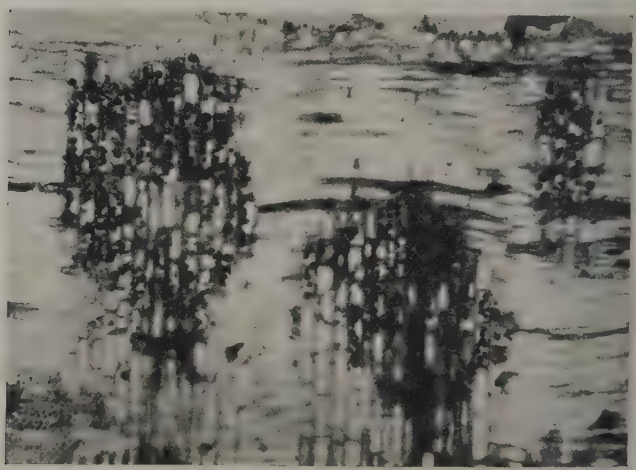


PLATE XXVIII.

Fig. 1.— Photomicrograph of a cross section of a portion of the sapwood of a bitternut hickory (*Hicoria minima*) log rotted by *Polyporus pargamenus*, showing a black zone in transverse section, X 100. The wood at the right has been thoroughly decayed as the appearance of the cell walls will testify. At the left the wood is in the earlier stages of decay and is giving rise to decomposition products upon the advance of the decay. In the center is shown a black zone which separates the portions of wood in the different stages of decay.

Fig. 2.— Photomicrograph of a radial section of a portion of the sapwood illustrated in Plate XXVII, showing the formation of the brown drops of decomposition products in the pith-ray cells, X 100. The photograph was made of a portion of wood lying approximately one-half cm. within the external infiltrated portion.

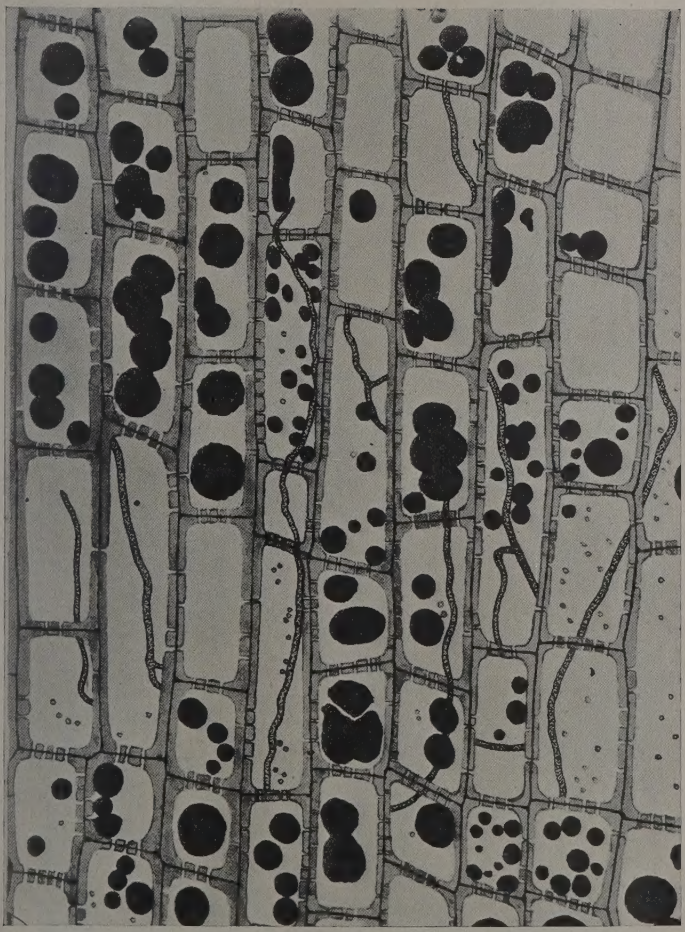


PLATE XXIX.

Camera lucida drawing of a pith-ray illustrated in Plate XXVIII, Fig. 2, showing in detail the formation of the brown drops of the decomposition products in the pith-ray cells, X 650. Occasional fine fungal hyphæ may be seen passing through the simple pits in the end walls of the pith-ray cells.

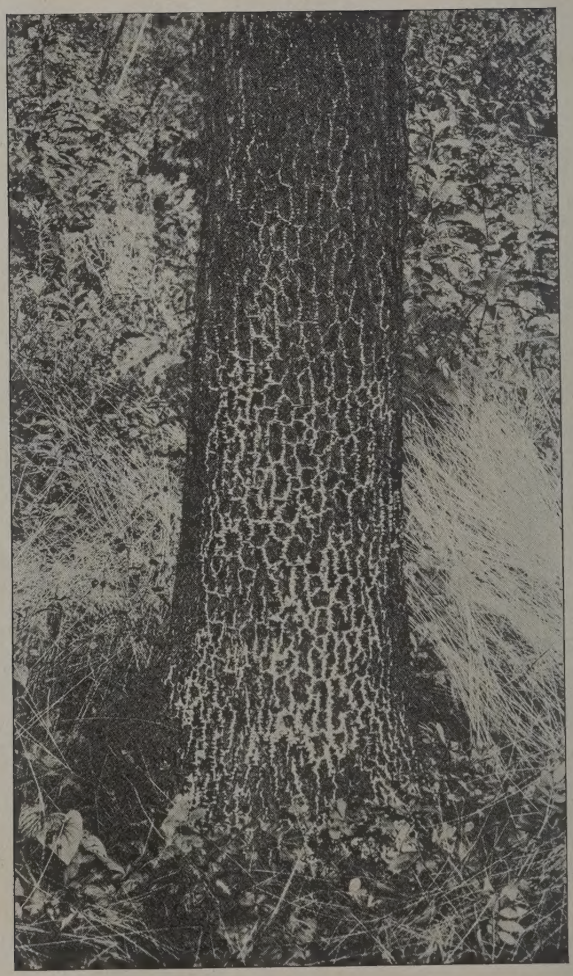


PLATE XXX.

Appearance of the sporophores of *Polyporus pargamenus* on a scarlet oak (*Quercus coccinea*) 1 year and 3 months after the tree was killed by a light surface fire.

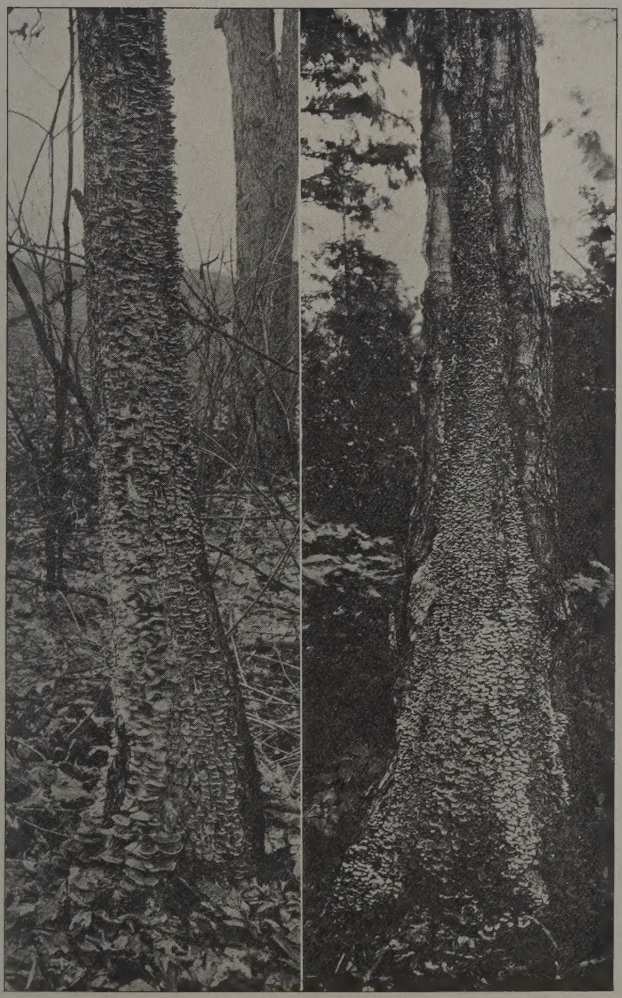


Fig. 1. Fig. 2.

PLATE XXXI.

Fig. 1.— Luxuriant growth of sporophores of *Polyporus pargamenus* on a dead white oak (*Quercus alba*) trunk.

Fig. 2.— A fire-scarred white oak (*Quercus alba*) that continued to grow vigorously despite the injury. The dead wood, however, was infected by *Polyporus pargamenus* in the meantime and is now badly decayed, although the tree is still living.